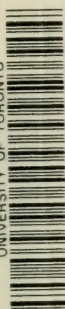


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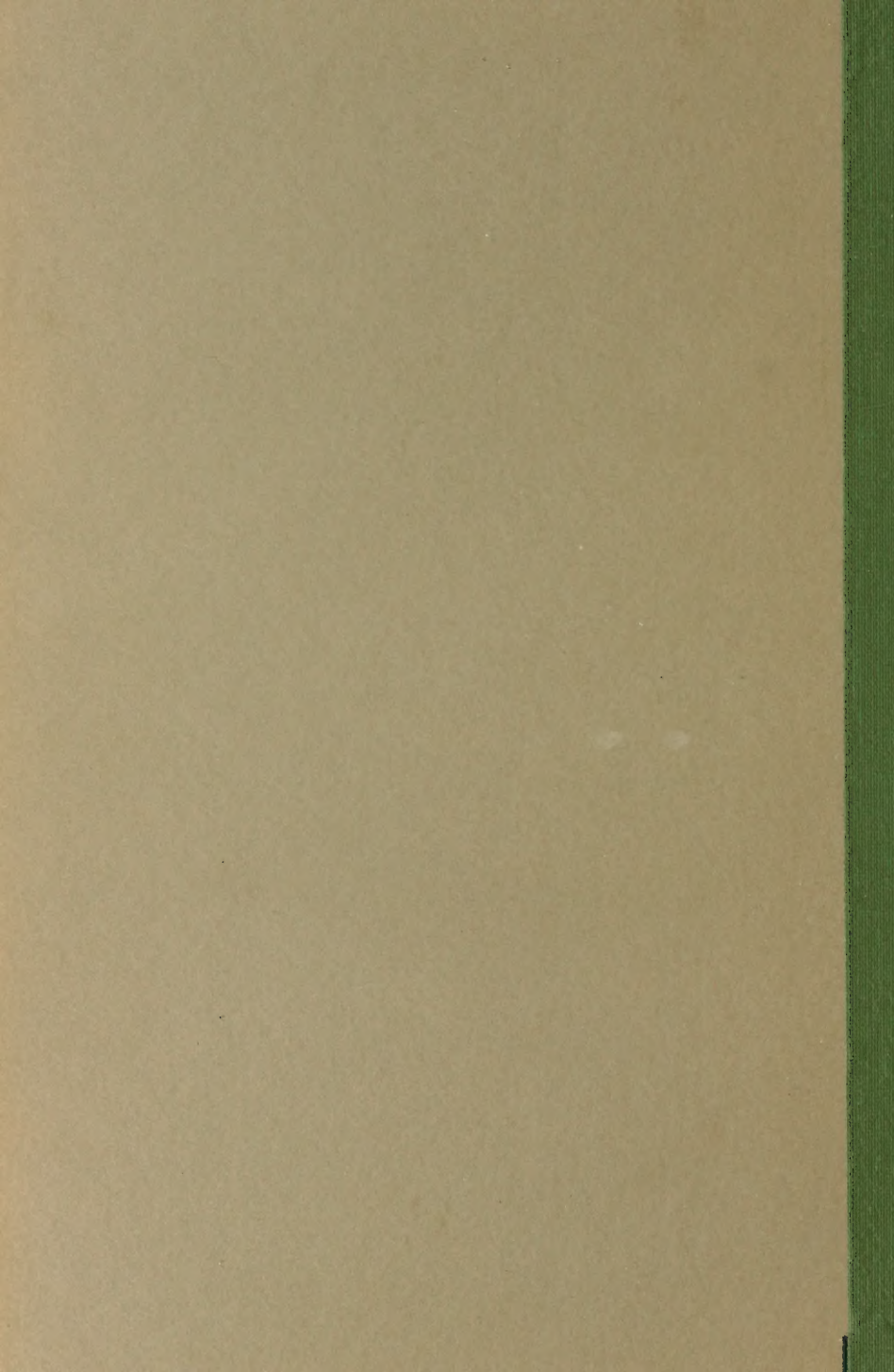
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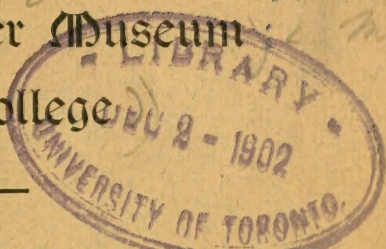




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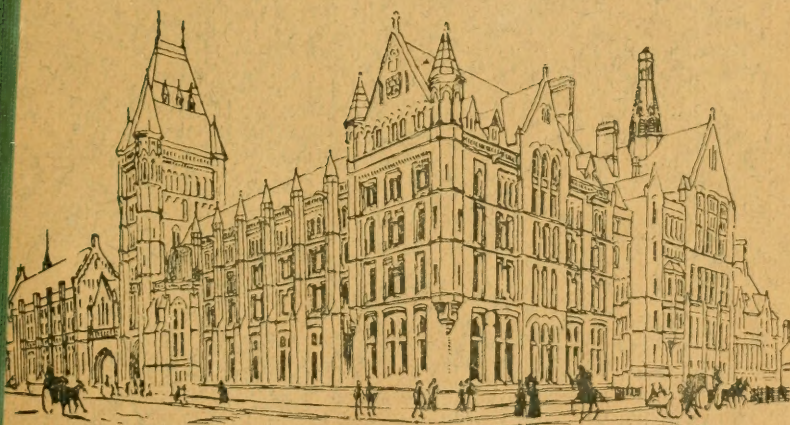
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[No. 7]



*2d. ed., rev. & extended*

## DESCRIPTIVE CATALOGUE

OF THE

## EMBRYOLOGICAL MODELS

BY

Professor S. J. HICKSON, D.Sc., F.R.S.

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DESCRIPTIVE CATALOGUE  
OF THE  
EMBRYOLOGICAL MODELS

BY THE LATE

A. MILNES MARSHALL, M.A., M.D., D.Sc., F.R.S.

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SECOND EDITION

*Revised and Extended by*

SYDNEY J. HICKSON, M.A., D.Sc., F.R.S.,

*Professor in the Victoria University ;  
Beyer Professor of Zoology in Owens College.*



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Description of a Series of Wax Models illustrating  
the Early Stages of Development of

## AMPHIOXUS.

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### CASE XLI.

*The Models are by Dr. A. Ziegler, from the drawings and descriptions of Professor Hatschek.\**

*The models are in each case about 400 times the linear dimensions of the natural objects.*

The spawning period commences in early spring, towards the end of March, and continues throughout the summer. The eggs are laid by the female in the evening, about an hour after sunset, and are fertilised at once by spermatozoa shed over them by the male. Development commences about an hour after fertilisation is effected, and proceeds with great rapidity: by sunrise on the following morning the embryo has reached the stage shown in model **13**, at which period it works its way out of the egg membrane, and swims freely. Twenty-four hours later it has reached the stage shown in models **23** to **25**: and a few hours later still, *i.e.*, about thirty-six hours from the time of fertilisation, the mouth and first gill cleft are formed.

The extreme rapidity with which the early stages of development are passed through is to be associated with the very small size of the egg, and the small amount of food yolk present in it.

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\* Hatschek, "Studien über Entwicklung des Amphioxus," *Arbeiten Zool. Inst. Wien*, vol. 4, 1881; See also E. W. MacBride, "The Early Development of Amphioxus," *Quart. Journ. Micr. Sci.*, vol. 40, p. 589-612, pl. 43-45, 1898.

Three periods may conveniently be distinguished in the early embryonic development :—

**Period I.**—Segmentation of the egg, and formation of the blastula : illustrated by models **1 to 8**.

**Period II.**—Formation of the gastrula and closing of the blastopore : illustrated by models **9 to 12**. At the close of this period the embryo becomes free.

**Period III.**—Formation of the nervous system, and of the myotomes and notochord. Models **13 to 25**.

The colours of the models have the following significance :—

**Grey** : stages in the segmentation of the egg.

**Blue** : epiblast.

**White** : neural plate, and neural tube.

**Red** : hypoblast.

**Dark Red** : mesoblast.

**Crimson** : notochord.

## PERIOD I.—SEGMENTATION OF THE EGG AND FORMATION OF THE BLASTULA.

### MODELS 1 TO 8.

The **ovum**, or egg, of *Amphioxus* is about 0·1 mm. in diameter. It is invested by a delicate **vitelline membrane**, which at first surrounds the egg closely, but separates from it directly after fertilisation is effected. The egg is somewhat opaque owing to the yolk granules imbedded in it. Segmentation is complete and very nearly uniform, and the stages shown in models **1 to 8** are completed in three to four hours from the time of fertilisation.

**MODEL 1. Ovum before fertilisation.**—The small bead on the top is the **polar globule**. From analogy with other animals it is probable that there are really two polar bodies represented in this single globule.

**MODEL 2. Two-celled stage.**—The ovum, after fertilisation, has divided, by a vertical cleft, into two halves of equal size.

**MODEL 3. Four-celled stage.**—By a second vertical cleft, at right angles to the first, each of the two cells of the preceding stage

is divided into two. The four cells are of equal size, and remain in close contact with one another.

**MODEL 4. Eight-celled stage.**—By a horizontal or equatorial cleft each of the four cells of stage 3 is divided into two. The four upper cells are rather smaller, and contain rather fewer yolk granules than the four lower cells. The polar globule is still seen on the top of one of the upper tiers of cells.

**MODEL 5. Sixteen-celled stage.**—By two vertical clefts at angles of  $45^\circ$  to the two former vertical clefts, each of the eight cells of stage 4 is divided into two equal parts, and the number of the cells is again doubled. The embryo now consists of an upper tier of eight smaller cells, and a lower tier of eight larger cells.

**MODEL 6. Stage with thirty-two cells:** bisected and one half removed. By two new horizontal clefts each of the tiers of cells of stage 5 is divided. The embryo now consists of thirty-two cells arranged in four tiers, each of eight cells. The cells of the lowermost tier are distinctly larger than those of the other three. The central space, or **segmentation cavity**, is now almost closed by approximation of the cells of the upper and lower tiers respectively.

**MODEL 7. Blastula stage:** bisected and one half removed. The cells have increased in number by further division. The cells round the equator are represented in the act of dividing horizontally. The **segmentation cavity** or **blastocœl** is now closed above, but is still open at its lower pole.

**MODEL 8. Completed blastula stage:** bisected and one half removed. The **blastocœl** is now completely closed: the embryo being in the form of a hollow ball with a wall composed of a single layer of cells. The cells have increased considerably in number, and in the upper half have assumed a definite columnar shape, with flattened sides and ends. At the lower pole the wall consists of larger cells (red) with rounded ends. The smaller (grey) cells become the **epiblast**, the larger (red) cells the **hypoblast** of the next stage.

## PERIOD II.—THE GASTRULA STAGE.

### MODELS 9 TO 12.

The **hypoblast** cells forming the lower pole of the blastula become flattened and invaginated within the epiblast cells, the



embryo thus acquiring the cup-shaped **gastrula** form. The cavity of the cup, or **archenteron**, lined by hypoblast, becomes the alimentary canal: the mouth of the cup or **blastopore**, narrows very considerably, but remains open throughout the period.

This period occupies about six hours: at its close the embryo liberates itself from the vitelline membrane and swims freely.

**MODEL 9. Commencing gastrula stage:** bisected and one-half removed. The hypoblast (red) is becoming doubled up within the epiblast (blue). The **blastocœl** or **segmentation cavity** is still of considerable size.

**MODEL 10. Gastrula:** right half. The **Segmentation cavity** is obliterated by the invaginated hypoblast coming in contact with the epiblast. The **blastopore** or gastrula mouth is of large size.

**MODEL 11. Gastrula:** right half. The **blastopore** has become greatly reduced in size, as compared with stage **10**: it marks the posterior end of the embryo. The **dorsal surface**, the right hand side in the model is flattened: the opposite or **ventral surface** is strongly convex. In the living embryo each of the epiblast cells bears at this stage a flagellum, not shown in the model: and by lashing movements of these flagella the embryo rotates within the vitelline membrane.

**MODEL 12. Completed gastrula:** right half. The embryo has elongated considerably, and is now egg-shaped. The **blastopore** has narrowed still further, and is now a small aperture at the posterior end, slightly on the dorsal surface, and leading into the **archenteron** or primitive alimentary cavity. The dorsal surface of the embryo is flat, the ventral surface convex. At this stage the embryo works its way out of the vitelline membrane and commences its free existence, swimming with the anterior end first, and the blastopore behind. Swimming is effected by the flagella which cover the surface in this and in all the subsequent stages shown by the models.

[According to MacBride the polar cells shown in this model do not exist.]

## PERIOD III.—THE FREE SWIMMING LARVA.

## MODELS 13 TO 25.

The chief events that occur during this period are the formation of the tubular **nervous system** and the **neurenteric canal**; the formation of the **myotomes** from the archenteron; and the formation of the **notochord** from the hypoblast of the mid-dorsal wall of the archenteron.

[According to MacBride the mesoblast originates as a series of true gut pouches, viz., one anterior unpaired pouch and two pairs of lateral pouches. Of these the first divides to form the two head cavities: the anterior pair give rise to the first pair of myotomes, and in addition, to two long canals extending back ventrally: the posterior pair are gradually separated from the gut, and *pari passu* divided into a series of myotomes.]

The chief peculiarity is the fact that throughout the period the sole communication of the archenteron, or primitive gut, with the exterior is through the tube formed by the nervous system.

The period occupies about twenty-four hours, and terminates with the formation of the mouth at a stage slightly older than that shown in model 25.

**MODEL 13.** The right half of a free-swimming embryo at the commencement of the period: part of the epiblast of the right side has been removed.

The embryo is increased in length. The flattening of the dorsal surface is very marked, and the median flattened area, or **neural plate**, is separated by a groove from the lateral epiblast. The first **myotome** of the right side is exposed by removal of the epiblast covering it: it is a slight pouch-like outgrowth of the archenteron, bounded in front and behind by shallow grooves. The **blastopore** is now very narrow.

**MODEL 14.** The right half of an embryo showing the formation of the **neural tube** and **neurenteric canal**.

The **neural plate** (white) has become slightly depressed so as to form the floor of a longitudinal **neural groove** along the back of the embryo. The epiblast (blue) along the sides of the groove

forms ridges, which, at the posterior end of the embryo, have grown in towards each other, and have met and fused so as to roof over the blastopore and the hinder end of the neural groove. The **blastopore** no longer opens directly on the surface, but forms the **neurenteric canal**, connecting the archenteron with the neural groove. Two pairs of mesoblastic somites are present at this stage : and are better seen in model **16**.

**MODEL 15.** The middle portion of an embryo of the same age as the last. The black lines on the outer surface of model **14** indicate the part cut out.

On the dorsal surface the **neural groove** is seen deepening posteriorly, and opening near the hinder end of the model into the **neural tube**.

**Anterior end of the section.** The **neural plate** (white) lies on the dorsal surface : it is overlapped by the lateral epiblastic plates (blue), which have not quite met in the median plane. The Section passes through the anterior pair of **myotomes**, which arise as hollow diverticula (dark red) from the dorsal and lateral angles of the **archenteron**.

**Posterior end of the section.** The section is of larger size, passing through the widest part of the embryo. The **neural plate** (white) is completely covered by the lateral epiblastic plates (blue), which have met and fused in the median plane. The **neural canal** lies in the median plane between the epiblast and the neural plate. The section passes through the hinder part of the **archenteron** (red), at the dorso-lateral angles of which are a pair of commencing myotomes.

**MODEL 16.** The dorsal half of an embryo of the same age as models **14** and **15**.

**Ventral surface.** In the anterior half of the embryo two pairs of **myotomes** are seen arising as lateral pouchings of the **archenteron**. At the posterior end of the embryo are shown two rounded **polar cells** [the existence of which has recently been denied] : and just in front of these, in the roof of the archenteron is the entrance to the **neurenteric canal**.



**Dorsal Surface.** The epiblast has been removed from the middle and left side of the model. A wire has been passed along the **neural canal** and emerges in front through the **neuropore**. On the left side the two **myotomes** (red) are well seen, separated from one another by grooves. In the middle of the model the part of the dorsal wall of the **archenteron** from which the **notochord** will be developed is exposed by removal of the neural plate.

**MODEL 17.** The right half of an embryo with six pairs of myotomes. The black lines on the outer surface indicate the planes of section of models **18, 19** and **20**. The neural canal is closed along nearly the whole length of the embryo; its external opening, the **neuropore** being only a short distance from the anterior end of the embryo. At its hinder end the neural canal communicates through the neurenteric canal with the archenteron. In the archenteron the openings of the six mesoblastic somites of the right side are seen. The anterior end of the archenteron is slightly widened and prolonged dorsally.

**MODEL 18.** Portion of the anterior half of an embryo of the same age as No. **17**: the two anterior transverse lines on the model **17** indicate the planes of section.

**Anterior end of the section.** The plane of section passes through the **neuropore**, below which the **neural plate** (white) is seen. The **archenteron** (red) is cut in front of the first pair of **myotomes**.

**Posterior end of the section.** The plane of section passes between the first and second pairs of myotomes; the posterior surfaces of the first pair being seen as two lateral masses of cells (red) between the neural plate and the archenteron. The longitudinal fold of the mid-dorsal wall of the archenteron is the commencing **notochord** (crimson). The **neural plate** is grooved dorsally, and its two halves slightly folded on each other.

**MODEL 19.** Portion of the posterior half of an embryo of the same age as No. **17**: the two posterior transverse lines on model **17** indicate the planes of section.

**Anterior end of the section.** The plane of section passes through the middle of the **fourth pair of myotomes** (dark red),

which are seen as two lateral outgrowths from the dorsal surface of the **archenteron**, and still communicating with this by narrow apertures. The **neural plate** is grooved dorsally, and its two sides folded longitudinally. The mid-dorsal wall of the archenteron is just commencing to be folded on itself to form the **notochord**.

**Posterior end of the section.** The plane of section is posterior to the last or sixth pair of myotomes. The **neural plate** is flat and very wide.

**MODEL 20.** The dorsal half of an embryo of the same age as No. 17. The plane of section is indicated by the horizontal line on model 17.

On the ventral surface the enlarged anterior end of the **archenteron** is seen in front: behind it are six pairs of **myotomes**: the hindmost or sixth pair not yet completely formed. At the posterior end of the model is the **neurenteric canal**: a wire has been inserted into it; the anterior end of the wire is seen on the dorsal surface of the model projecting through the **neuropore**.

**MODEL 21.** The dorsal portion of the body of an embryo with seven pairs of **myotomes**. The anterior end of the embryo has been removed by a transverse section through the middle of the first pair of somites: and the ventral half of the embryo by a horizontal section at the level of the widest part of the archenteron. A wire has been passed along the **neural canal**, and its lower end projects through the **neurenteric canal** into the **archenteron**.

The first pair of **myotomes** is seen at the anterior end of the model: they have completely separated from the archenteron, and are growing towards the ventral surface of the embryo, between the epiblast and the hypoblast. The **notochord** (crimson) is seen at the anterior end of the section as a longitudinal fold of the mid-dorsal wall of the archenteron, immediately below the neural plate: further back in the model the notochord is less conspicuous.

**MODEL 22.** A segment cut from an embryo with eight pairs of myotomes. The section at the larger end of the model passes through the middle of the first pair of myotomes; that at the smaller or hinder end through the fifth pair.

The **neural plate** is folded longitudinally, but the roof of the neural groove or canal is still formed by the external epiblast alone.

The **myotomes** have completely separated from the archenteron, and are growing down the sides of the embryo between the epiblast and the gut.

The **notochord** (crimson) is a longitudinal fold of the mid-dorsal wall of the archenteron ; the two sides of the fold are now in contact with each other.

**MODEL 23.** An embryo with nine pairs of myotomes. The epiblast has been removed from the left side to expose the myotomes, the neural tube and the anterior end of the notochord.

The **neuropore** is on the dorsal surface, close to the anterior end of the embryo : it leads into the neural tube (white). The outlines of the **myotomes** are indicated by grooves. The anterior somite is the largest, and from its dorsal and anterior angle a conical anteriorly directed diverticulum extends forwards almost to the anterior end of the embryo. Immediately below this diverticulum is a pouch-like outgrowth from the archenteron, which at a later stage separates from the archenteron, becomes ciliated, and acquires an opening to the exterior. The myotomes diminish in size from before backwards ; behind the ninth is a tract from which additional myotomes will be formed during the later stages.

The extreme anterior end of the **notochord** is seen in the model in front of the neural tube and lying on the roof of the archenteron.

**MODEL 24.** The middle portion of the body of an embryo of the same age as No. 23. A wire is passed along the neural canal.

**Anterior end.** The plane of section passes through the middle of the fourth pair of mesoblastic somites or myotomes.

The **neural canal** is now completed, the side walls having grown in and met each other so as to form a roof to the canal, independent of the external epiblast.

The **archenteron**, or gut, is approximately circular in outline.

The **notochord** (crimson) is a solid rod of cells, completely separate from the gut wall.



The **myotomes** have extended rather more than half way down the sides of the gut. The cells of the inner wall of each myotome, opposite the notochord, have enlarged and become modified to form **muscle fibres**, running parallel to the notochord, and seen cut across in the model.

**Posterior end.** The roof of the **neural canal** is in the act of being formed, by growth of the side walls towards the median plane. The plane of section passes through the **hindmost pair of myotomes**, which are still in the form of hollow pouches opening into the gut cavity. The **notochord** (crimson) is a fold of the mid-dorsal wall of the gut, the two halves of which are a little distance apart.

**MODEL 25.** The right half of an embryo of the same age as No. 23.

The **neuropore**, on the dorsal surface of the anterior end of the body, leads into the neural canal (white), which runs the whole length of the embryo, and opens behind through the **neurenteric canal** into the hinder end of the **archenteron** or gut. The **notochord** (crimson) is a longitudinal rod lying between the neural tube and the gut, and extending forwards a short distance in front of the neuropore.

The slight depression on the ventral surface of the archenteron, about an inch and a half from the anterior end of the model, marks the place where the **first gill slit** will be formed, in the mid-ventral plane, at a slightly later stage.

A few hours later than the stage illustrated by models 23 and 25, and about 30 hours from the time of fertilisation, the embryonic period comes to an end. At this stage 14 pairs of myotomes are present, and the mouth and first gill slit appear. From this time development proceeds much more slowly.

It is worthy of special notice that up to the close of the embryonic period the sole communication of the alimentary canal, or archenteron, with the exterior is through the neurenteric canal and the central canal of the nervous system. Whether any food ever enters by this path is, however, extremely doubtful: and it is probable that the whole development up to this stage is effected at the expense of the yolk granules present in the egg.

# Description of a Series of Wax Models illustrating the Development of the TORPEDO.



## CASE XLI.

*The Models were made by Mr. Friedrich Ziegler from numerous photographs of the embryos. They are intended to illustrate the account of the Development of Torpedo given by Dr. Ziegler and Mr. F. Ziegler.\**

*The Models are about sixty times the linear dimensions of the natural objects.*

**MODEL 1. Stage B.** This is a view of the blastoderm as seen from above. At the posterior end is seen the **embryonic rim**, which is slightly raised above the yolk. This **embryonic rim, ER**, gradually flattens out at the sides and anterior end. In the middle of the thickest part of the rim is seen the first rudiment of the embryo, **E**. Near the anterior end of the blastoderm is seen the swelling which marks the remnant of the segmentation cavity, **SC**.

**MODEL 2. Stage C.** The embryo is considerably larger than in Stage **B**. The medullary folds, **MF**, are well seen. They widen out in front to form the rudiment of the brain. At the hind end of the embryo are seen the pair of tail swellings, **TS**.

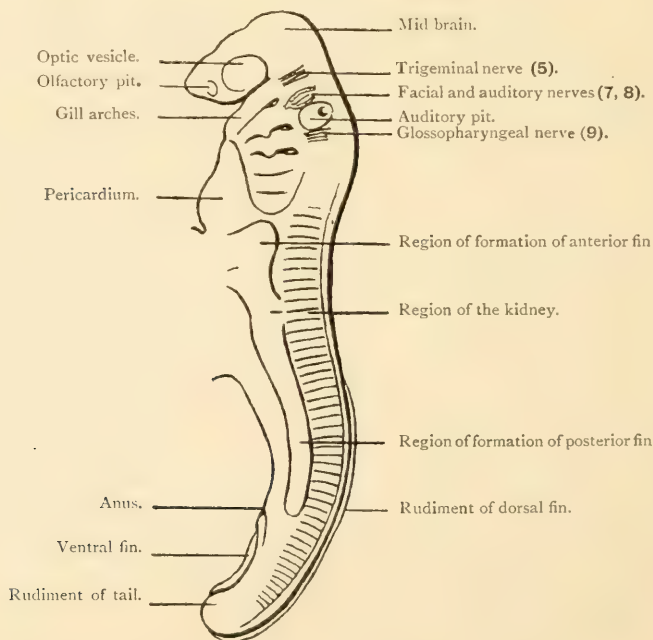
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\* Ziegler, H. E. & F., "Beiträge zur Entwicklungsgeschichte von Torpedo," *Archiv f. anat. Anat.*, vol. 39, p. 50-102, pl. 3, 4, 1892.

**MODEL 3. Stage D.** The medullary folds at this stage are much more strongly marked, and the medullary groove, **MG**, much deeper. At the posterior end, the medullary groove runs into a deep fold between the tail swellings which closes to form the neurenteric canal, **NC**. The head of the embryo is now clearly indicated by an enlargement at the anterior end.

**MODEL 4. Stage F.** The medullary canal is now partly closed, but remains open at the head and tail regions. The tail swellings have elongated and begun to fuse together. They project considerably beyond the posterior border of the blastoderm. On the body of the embryo may be seen the projections caused by the **Eyes** and the swelling in the gill region of the neck, **GR**. A certain number of protovertebræ, **PV**, are also indicated on the sides of the body.

**MODEL 5. Stages J-K.** The medullary canal is now closed, but the roof is thin in the brain region. The following organs can be seen:—





## Description of a Series of Wax Models illustrating the Development of the FROG.

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### CASE XXXIII.

*The Models are by Dr. A. Ziegler, from the drawings and under the direction of Professor Ecker.\**

*The Models are in each case 16 times the linear dimensions of the natural objects.*

Frogs' eggs are laid in water about March or April. The eggs are invested by gelatinous envelopes, which stick together and swell up greatly in the water, forming the bulky masses known as frog's spawn.

The eggs are fertilised by the male as they are laid, and commence to develop about three hours later. The rate of development varies very greatly according to the temperature: in moderately warm weather the segmentation of the egg, models **1** to **10**, is completed in about four days, and the formation of the embryo commenced. In about a fortnight from the time of laying of the eggs the young tadpoles, models **19** and **25**, work their way out of the jelly by vigorous movements, and become free. A few days later the mouth is formed, and the tadpole begins to feed freely, and grows rapidly. The last stage shown in the series, model **22**, is that in which the gill clefts and the external gills are almost completely covered by the opercular folds, and the hind limbs are just appearing. During the third or fourth month the metamorphosis occurs, by which the tailed gill-breathing tadpole becomes converted into the tailless lung-breathing frog.

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\* Ecker, "Icones Physiologicae," 1851 to 1859.

Marshall, "Vertebrate Embryology," p. 90-218, 1893.

Five chief periods are represented by the series of models.

**Period I.**—The segmentation of the egg: models **1** to **10**.

**Period II.**—The enclosure of the egg by the spreading epiblast: and the establishment of the germinal layers: models **11** and **12**.

**Period III.**—The formation of the embryo up to the time of hatching. Models **13** to **19**, and **23** to **25**.

**Period IV.**—The development of the tadpole after hatching. Models **20** to **22**.

**Period V.**—The metamorphosis of the tadpole into the frog. Models **26** to **29**.

## PERIOD I.—THE SEGMENTATION OF THE EGG.

### MODELS 1 to 10.

The stages shown in these models occupy between three and four days. The egg is in all the models placed on its side: in the natural condition the dark coloured half is uppermost, owing to its lower specific gravity.

**MODEL 1. The egg before the commencement of development.** The frog's egg is spherical, and about 2 millimetres in diameter. One half of the surface is of a dark brown or black colour, the opposite hemisphere being white. In the natural position the pigmented hemisphere is uppermost: the white hemisphere undermost, owing to its greater specific gravity. The egg contains a considerable quantity of **food yolk** in the form of **yolk granules** dispersed through its substance. These yolk granules are more abundant in the lower or white half than in the upper or pigmented half: they give the lower half of the egg its greater weight, and their presence serves to retard the processes of development in the lower as compared with the upper half of the egg.

The whole of the development up to, and a little beyond the time of hatching, model **19**, is effected at the expense of this store of food yolk.

**MODEL 2. Stage with two cells.** The egg is divided by a vertical constriction, which commences at the upper or pigmented pole, into two equal halves, which remain in close contact.

**MODEL 3. Stage with four cells.** By a second vertical cleft, at right angles to the first, each of the cells of the preceding stage is divided into two. The four cells are of equal size.

**MODEL 4. Stage with eight cells.** By a horizontal or equatorial cleft, each of the four cells of stage **3** is divided into two cells. The four upper, or pigmented cells, are much smaller than the four lower cells.

It must be remembered that the models are represented lying on their sides: so that what is really a horizontal cleft appears vertical in the model.

**MODEL 5. Stage with twelve cells.** Each of the four upper cells has divided into two. The four lower cells are just commencing to divide. This stage illustrates well the greater rapidity of the processes of development in the upper as compared with the lower half of the egg, due to the comparative freedom of the former from food yolk.

**MODEL 6. Stage with twenty-four cells.** Each of the four lower cells has divided into two: and by a horizontal cleft the upper cells are divided into two tiers, each of eight cells.

**MODEL 7. Stage with thirty-two cells.** The lower cells have divided horizontally. There are now four tiers, each of eight cells: the cells of the uppermost tier are much the smallest: those of the lowest tier much the largest.

**MODELS 8 and 9. Later stages.** The process of cell division has continued; the upper cells always dividing more rapidly, and so being of smaller size than the lower cells.

**MODEL 10. Egg at the close of segmentation.** The cells of the upper pole, or **epiblast cells**, are now of very small size. The lower pole consists of much larger, non-pigmented cells, which are laden with yolk granules, and may be termed **yolk cells**.

## PERIOD II. THE ENCLOSURE OF THE EGG BY THE EPIBLAST.

### MODELS 11 AND 12.

**MODEL 11.** The pigmented **epiblast cells** of the upper pole are now spreading over the white **yolk cells** so as to enclose them. The

margin of the spreading epiblast is approximately circular ; its upper half is sharply defined, but in the lower half the epiblast cells and yolk cells pass more gradually into each other. The **crescentic slit** between this sharply defined upper border and the yolk cells leads into a cavity in the egg, which is the **archenteron** or primitive gut.

**MODEL 12.** The **epiblast** has spread so as to cover the whole egg except a small circular spot, where the yolk cells still come to the surface. This circular hole is the **blastopore**, and the yolk cells filling it up form the **yolk plug**. The margin or lip of the blastopore is now sharply defined all round : and the circular groove between it and the yolk plug leads into the **archenteron**.

### PERIOD III. - FORMATION OF THE EMBRYO, AND DEVELOPMENT UP TO THE TIME OF HATCHING.

#### MODELS 13 TO 19, AND 23 TO 25.

**MODEL 13.** The **blastopore** is still further reduced in size, and is somewhat pyriform in shape : it is filled up by the **yolk plug** (white), and marks the hinder end of the embryo. From the upper lip of the blastopore a longitudinal groove, the **neural groove**, extends forwards along the dorsal surface, which is slightly flattened. A pair of low ridges, very indistinctly marked as yet, at the sides of the neural groove are the **neural folds**.

**MODEL 14.** The **blastopore** is closed, and the **yolk plug** no longer visible on the surface. The dorsal surface of the embryo is formed by the **neural plate**, a slightly depressed area, wider in front at the head end, and narrowing posteriorly : it is bordered laterally by the **neural ridges**, which at the anterior end are connected by a transverse ridge, marking the anterior limit of the brain. Along the neural plate in the median plane is the **neural groove**.

**MODEL 23.** The anterior half of the embryo of the same age as model 14 : the embryo has been divided transversely about the middle of its length.

The brown external layer is the **epiblast** : on the dorsal surface the **neural plate** and **neural folds** are seen in section.



The cavity in the interior of the embryo is the **archenteron** or primitive gut : its thin roof and sides are formed of **hypoblast** ; its floor by the solid mass of **yolk cells**.

**MODEL 15.** The whole embryo is more ovoidal in shape than before. The **neural ridges** have met each other in the body region but in the head are still some distance apart : they are connected together in front by a well-marked transverse ridge.

**MODEL 16.** The head and body are separated by an oblique lateral constriction. The neural folds have met along almost their entire length, but are still separate at the anterior end of the brain. A vertical groove on the side of the head at its widest part marks the position of the **first branchial cleft** : a shallow median depression on the under surface of the head just below the brain is the commencing **stomodæum** or mouth invagination : and a crescentic slit running across the ventral surface of the head immediately behind the stomodæum is the commencing **sucker**.

At the tail end of the embryo the median groove, formed by meeting of the two neural folds, can be traced round to the posterior surface of the commencing tail. In communication with its hinder end are two depressions : of these the dorsal one is the **blastopore**, leading into the archenteron and the neural canal : and the ventral one is the **proctodæum**, which at present is a blind pocket, but which at a later stage opens into the gut and becomes the **anal aperture**.

**MODEL 17.** Embryo, in which the head and body are clearly marked off from each other, and the tail is commencing to appear.

The **neural canal** is closed along its entire length, a median longitudinal groove marking the line of meeting of the two neural folds.

On the under surface of the head, in front, is the shallow **stomodæal depression**, below which is the prominent horse-shoe shaped **sucker**. The posterior or pharyngeal part of the head is very wide : the two vertical grooves crossing it mark the positions of the **first** and **second branchial clefts**, which, however, do not open until a much later period. The vertical ridge in front

of the first groove is the **hyoid arch**: the prominent ridge between the two grooves is the **first branchial arch**; and the smaller ridge behind the second groove is the **second branchial arch**.

In the body region the prominent ventral swelling lodges the greater part of the food yolk. At the hinder end of the body the groove between the neural folds can be traced to the circular **proctodæal** aperture.

**MODEL 24.** The left half of an embryo of the same age as model 17.

The external **epiblast** is brown. The **neural tube** is white: its anterior end is expanded to form the **brain**, in which slight constrictions indicate the commencing division into the brain vesicles. The posterior part of the neural tube, or **spinal cord** is narrower. At its hinder end the neural tube bends round the end of the notochord (blue) and communicates through the **neurenteric canal**, the remains of the dorsal portion of the blastopore, with the **archenteron**. The **notochord** (blue) is a longitudinal rod lying between the neural tube and the archenteron.

The **archenteron**, or primitive gut, is very wide in front, in the pharyngeal region, but is narrow in the body. At its hinder end it opens to the exterior through the **proctodæal aperture**, and also communicates, as already noticed, through the **neurenteric canal** with the neural tube.

The anterior wall of the **pharynx** is thin, and in contact with the floor of the shallow **stomodæal depression**. The short conical wedge of epiblast (brown), in the angle between the brain and the anterior wall of the pharynx, is the commencing **pituitary body**. The backwardly directed diverticulum from the floor of the hinder end of the pharynx is the commencing **liver**.

**MODEL 18.** Tadpole shortly before the time of hatching.

The head is larger and squarer than before, and the tail much more prominent. In the body region a well-marked longitudinal groove marks off the dorsal region from the ventral part lodging the food yolk.

The median dorsal groove, marking the line of fusion of the neural folds, has disappeared : the neural tube having completely separated from the external epiblast.

In the **head**, the lateral swellings near the anterior end are caused by the developing **eyes**. The **stomodæal depression** is much deeper than before, and the **sucker** on the ventral surface of the head much larger. Three visceral arches, the **hyoidean**, **first branchial**, and **second branchial**, form vertical ridges at the sides of the pharyngeal region : the vertical grooves separating them mark the positions of the **first** and **second branchial clefts**.

#### MODEL 19. Tadpole at the time of hatching.

Head, body, and tail, are now of about equal length ; and the yolk mass is considerably reduced in size.

The **head** is very square. The eyes, which have not yet reached the surface, form prominent swellings in the anterior end : below and in front of them are the olfactory pits. The stomodæum is deeper, and the sucker larger than before.

The first and second branchial arches bear small external gills (red) on their outer borders. The hyoid arch is a prominent ridge in front of the first branchial arch, but bears no gill : the rounded swelling immediately above the hyoid arch is caused by the ear.

The **trunk** is divided into muscle segments or myotomes, seen through the skin on the right side, and exposed on the left side by removal of a small piece of skin.

#### MODEL 25. The left half of a tadpole at the time of hatching.

The section is a sagittal one as regards the head and neck, but further back passes slightly to the left of the median plane.

The **brain** (white) is retort-shaped, the bulb being formed by the **fore-brain** ; and the neck by the **hind-brain**, which passes back into the **spinal cord**.

The **notochord** (blue) is shown in its anterior half : it underlies the neural tube, and stops in front beneath the floor of the fore-brain.

The **pituitary body** is a solid conical ingrowth of epiblast, wedged in between the under surface of the fore-brain and the pharynx: its tip lies in very close relation with the anterior end of the notochord.

The **pharynx** is the large cavity below the notochord: the three red lines in its wall mark the positions of the **three aortic arches**.

The **heart** (red) is a muscular tube lying in the pericardial cavity below the pharynx: from its anterior end the **aortic arches** of the **first three branchial arches** are seen arising.

## PERIOD IV.—DEVELOPMENT OF THE TADPOLE AFTER HATCHING.

### MODELS 20 TO 22.

MODEL 20. A tadpole with fully-developed external gills.

This is a very interesting stage, as although the tadpole has been hatched some days, and has increased considerably in size, yet the mouth is not yet formed. It has been suggested that the sucker may be an organ enabling it to absorb fluid food during this period.

The **head** differs little from the condition seen in model 19. The **olfactory pits** are rather larger than before, and the **sucker** has divided into right and left halves, completely separate from each other.

At the sides of the neck there are three pairs of branched **external gills**, arising from the **first, second, and third branchial arches** respectively. The gill of the third branchial arch is smaller than the other two and more dorsally placed. The vertical groove in front of the first branchial arch marks the position of the **first branchial cleft**, but neither this nor any other of the gill clefts are yet open.

In the **body** the food-yolk is almost completely absorbed, and the outlines of the myotomes are well seen.

The **tail** has grown very rapidly, and now forms nearly half the length of the tadpole. The myotomes extend to its end, and it is bordered by wide **dorsal** and **ventral fins**; the dorsal fin extending forwards a short distance along the body.



**MODEL 21. Tadpole shortly after the formation of the mouth.**

The shape of the tadpole has altered considerably ; the **tail** has grown, and now forms more than half the length of the animal.

In the **head**, the **mouth opening** has formed on the under surface of the head : it is bordered by **fleshy lips** bearing rows of **horny teeth**, within which lie a pair of **horny jaws**. Above the mouth are the apertures of the **olfactory pits**, now somewhat smaller than before ; and at the sides of the head are the **eyes**, which have now reached the surface. The two halves of the **sucker** are still present on the under surface of the head, some little distance apart.

The three pairs of **external gills** are still present, but are almost completely concealed by the **opercular folds**, which are flaps of skin growing backwards from the outer edges of the hyoid arches, boxing in the gills and fusing with the body wall behind them. On the right side the hinder part of the opercular fold has been cut away to expose the **external gills**. On the left side the opercular fold has been slit up longitudinally and the two halves turned up and down : the external gills have been removed, their stems alone remaining and the **internal gills**, bordering the branchial arches below the external gills, brought into view. The internal gills are vascular folds of the margins of the gill clefts : which latter acquire their openings to the surface about the time the mouth opening is formed.

**MODEL 22. Tadpole at the time of appearance of the hind limbs.**

The head and body together form an ovoidal mass half as long as the tail.

In the **head** the **eyes** are much more prominent than before : the **mouth** has moved forwards towards the anterior end of the head : it is bordered by **frilled lips** bearing rows of **horny teeth**, within which are the two powerful **horny jaws**. The **nostrils** are above the mouth, and are small. The two halves of the **sucker** are still present on the under surface of the head behind the mouth, but disappear shortly after this stage.

The **opercular folds** have fused along their hinder borders with the body wall, so as to box in the gills. A small **opercular aperture** is still present on the right side : and a larger one, through which the tips of the external gills are projecting, on the left side.

At the base of the tail the commencing **hind-limbs** are seen as a pair of small rounded buds. Below and behind the limb buds is a conical prolongation of the body containing the **rectum**, which opens somewhat obliquely on the ventral edge of the tail.

The **tail** itself is of great size and strength : the dorsal fin especially being much larger than before. The stage represented in model 22 is generally reached about four or five weeks from the time of laying of the eggs.

## PERIOD V. THE METAMORPHOSIS OF THE TADPOLE INTO THE FROG.

### MODELS 26 TO 29.

*The four models of this series are by R. Brendel, and illustrate the changes in external form that occur during the transformation.*

**MODEL 26.** Tadpole a short time before the metamorphosis.

The **hind limbs** have increased considerably in length, and their several joints and the five toes are well established. The **fore limbs** are also well developed, but are not visible externally, being still contained within the opercular cavity ; the swellings caused by them are seen in the model at the anterior end of the body, just behind the head. The **mouth** is small, on the under surface of the head : it is provided with powerful **horny jaws**, used by the tadpole for cropping the aquatic plants on which it chiefly feeds.

At this period, about the end of the second month, the tadpole is breathing by both **gills** and **lungs** : the **lungs** are of considerable size, and the tadpole frequently comes to the surface of the water to take fresh air into them. The **gills** are rather smaller than in the earlier stages, and are already beginning to shrivel.

**MODEL 27.** Young frog during the metamorphosis.

The **hind-limbs** have increased considerably in size ; and the **fore-limbs** have broken through the skin by which they were

covered. The **horny jaws** of the tadpole are thrown off, the mouth-opening is becoming greatly widened, and the **tongue** is now of large size. The **gills** have become shrivelled up and massed together, and are no longer of any use for breathing. Besides the changes in the mouth, the entire alimentary canal is undergoing great modification, the stomach and liver are enlarging, and a new intestine shorter than the previous one is being formed. During these changes in its digestive organs the animal is unable to feed, and lives at the expense of its tail, which becomes rapidly shorter and shorter.

**MODEL 28. Young frog just before the close of the metamorphosis.**

The tail is now almost completely absorbed, a small stump alone remaining, and the metamorphosis is practically completed.

**MODEL 29. Young frog after the completion of the metamorphosis.**

The frog has now the form and structure of the adult : the tail has entirely disappeared : the mouth-opening is of great width : the changes in the digestive organs are completed ; and the frog is once more able to feed.

# Description of a Series of Wax Models illustrating the Development of the CHICK.

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## CASE LIV.

*The models are by Dr. A. Ziegler, from the drawings and under the direction of Professor His.\**

*The models are in each case 40 times the linear dimensions of the natural objects.*

In the descriptions, "anterior end" always refers to the anterior or head end of the embryo, which is directed upwards in all the models.

The ages given in the descriptions are approximate only, as there is considerable individual variability in the rate of development of chick embryos, especially during the early stages.

The hen's egg, as laid, consists of (1) the outer calcareous **shell**; (2) the **shell membrane** lining the shell; (3) the **white** or albumen; (4) the yellow **yolk**, enclosed in an elastic vitelline membrane.

Of these the **yolk** alone is the true egg, or ovum, and is the only part formed in the ovary; the remaining parts being accessory, and formed round the yolk as it travels down the oviduct towards the exterior.

The yolk of the hen's egg, like the ovum of other animals, is really a single cell, its great size being due to distension by granules of food matter, which are imbedded in its substance in enormous numbers.

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\* His, "Unsere Körperform," 1874,

Marshall, "Vertebrate Embryology," p. 219-340, 1893.



The egg is fertilised directly after leaving the ovary, and is developing during the whole time of its passage down the oviduct, which occupies from 12 to 20 hours in different cases. After the egg is laid development stops, but it recommences directly the egg is kept at the proper temperature, which, in the natural condition of things, is effected by the hen sitting on it. The total period of development is three weeks, the chick hatching as a rule on the twenty-first day of incubation.

Before the egg is laid, whilst it is travelling down the oviduct towards the exterior, it passes through the early stages of development. **Segmentation** does not involve the whole egg, but is limited to a small circular patch on the part of its surface, measuring about 3 mm. in diameter. This becomes divided up into cells, which soon become arranged in two layers, forming the **blastoderm**. At the time the egg is laid, the blastoderm forms a thin circular disc, about 3 mm. in diameter, lying like an inverted watch glass on the surface of the yolk. After the commencement of incubation the blastoderm begins to enlarge, spreading at its margin and gradually growing round and enclosing the yolk. The blastoderm, while still a circular disc, consists of an outer thicker marginal ring, the **area opaca**; and a central thinner and more transparent patch, the **area pellucida**. It is from the central part of the area pellucida, or **embryonal area**, that the embryo chick is formed, as shown in the models.

The models illustrate the development during the first four days of incubation.

### MODEL 1. Chick Embryo about the 20th hour of incubation.

#### DORSAL SURFACE.

The embryonal area or central part of the blastoderm, from which the embryo is formed, is marked off from the peripheral part by a marginal groove: this is shallow along the sides, deeper in front and behind where it forms the **head fold**, **HF**, and **tail fold**, **TF**, respectively.

The head end of the embryo forms a prominent rounded swelling at the anterior end of the embryonal area, projecting slightly above

the general level of the blastoderm. A median longitudinal groove runs almost the whole length of the embryonal area: the anterior third of this groove is the **neural groove, NG**, the first commencement of the nervous system: the posterior two-thirds form the **primitive groove, PG**, which does not give rise directly to any structure in the adult. The neural groove and primitive groove are really independent structures, but the distinction between them is not shown in the model.

#### VENTRAL SURFACE.

The marginal part of the model, coloured green, is the **area opaca, AO**, of the blastoderm. The central yellow portion is the **area pellucida, AP**, from the median portion of which, or **embryonal area**, the embryo is developed.

#### MODEL 2. Chick Embryo of about 23 hours.

##### DORSAL SURFACE.

The embryo has increased in size, and its outline is more clearly defined than in Model 1. By deepening of the head-fold, the anterior end of the head is lifted up distinctly above the level of the blastoderm.

The axial part of the embryo, white in the model, is formed by the nervous system and the primitive streak.

The **neural groove** has deepened considerably, especially in front. The **neural folds, NF**, bounding the groove at the sides, are prominent ridges which in the region of the hind-brain have grown in towards each other and almost met.

The posterior part of the white area in the model, rather less than half its entire length, is the **primitive streak, PS**, marked longitudinally by the **primitive groove**.

The distinction between the neural groove and primitive groove is not shown in the model.

The lateral swellings of the blastoderm, opposite the anterior end of the embryo, mark the anterior limit to which the **mesoblast**, or middle germinal layer, has extended: in front of these swellings the blastoderm consists of two layers only, **epiblast** and **hypoblast**. This two-layered portion is spoken of as the **proamnion, PA**.

In embryos of this age, three or four pairs of protovertebræ are already present, but are not shown in the model.

#### VENTRAL SURFACE.

The **area opaca** of the blastoderm is coloured green, the **area pellucida** yellow.

The central, depressed area, bounded by the outer pair of dark yellow lines is the **mid-gut**: this becomes deeper in front, and extends forward into the head-fold as a pocket-like sac, the **fore-gut, GF**.

### MODEL 3. Chick Embryo of about 29 hours.

#### DORSAL SURFACE.

The head-fold has deepened considerably, and the head of the embryo is now clearly defined.

The **neural folds** have met and fused with each other, so as to complete the **neural tube**, along the greater part of the length of the embryo. The neural folds are still separate at the extreme anterior end of the head, causing the median split seen in the model; and at the hinder end of the embryo they diverge so as to bound a lozenge-shaped patch, the **sinus rhomboidalis, SR**, white in the model. Behind the sinus rhomboidalis the **primitive streak, PS**, and **primitive groove** are shown white: in the model they are about an inch in length, and the line of demarcation between them and the neural folds and groove is not indicated.

Nine pairs of **protovertebræ** are present as small cubical masses of mesoblast, lying along the sides of the neural tube in the body region of the embryo. They are represented in the model as though seen through the epiblast.

A pair of very shallow depressions, just in front of the most anterior pair of protovertebræ, are the first commencements of the **auditory vesicles, AV**, or ears.

The prominent swellings of the blastoderm at the sides of the head mark, as in Model 2, the limit to which the mesoblast has extended forwards. In the deep pit of the blastoderm, or **proamnion, PA**, in which the head lies, there are as yet only

two layers, epiblast and hypoblast. The prominent crescentic fold forming the anterior boundary of this pit is the commencing **amnion, AN.**

#### VENTRAL SURFACE.

The **area opaca** of the blastoderm is coloured green ; the **area pellucida** yellow.

The median, depressed area, bounded by the outer pair of darker lines is the **hind-gut** ; and the deep pit into which this leads in front is the **fore-gut, GF.**

#### MODEL 4. Chick Embryo of about 29 hours.

The anterior part of the blastoderm has been removed, to expose the head fully : and on the ventral surface the floor of the pericardial cavity has been in part removed to expose the heart.

For a general description see Model 3.

#### VENTRAL SURFACE.

The under surface of the head is exposed by removal of the blastoderm. The anterior end of the neural groove is still open, and extends round to the ventral surface of the head.

The shallow depression on the under surface of the head, just in front of the cut edge of the blastoderm, is the commencing **stomodæum**, or mouth invagination, **ST.**

The **pericardial cavity** has been opened by removal of a portion of its ventral wall or floor, and the **heart** exposed. The pale-red portion in the model is the mesoblast which lines the pericardial cavity, and forms the outer wall of the heart. The longitudinal groove in the median plane marks the line of meeting of the walls of the two halves of the pericardial cavity, which are at first distinct from each other.

The two bright red tubes lying on the cut lower edge of the pericardial wall are the **vitelline veins**, which return blood charged with yolk from the vascular area of the blastoderm to the embryo : on entering the embryo they turn forwards, and lie side by side in the floor of the fore-gut, forming the two halves, right and left, of the heart, which are at first distinct from each other.



### MODEL 5. Chick Embryo of about 29 hours.

A longitudinal vertical section has been made along the line of the outer border of the protovertebræ of the right side, and the right half of the section removed. The epiblast has further been removed from the right half of the embryo so as to expose the brain, the protovertebræ, the heart, and the aorta.

For the external characters of the embryo see model 3.

The **nervous system** (white) consists of an anterior wider part, the **brain**, extending back to about the level of the first protovertebræ: and a posterior narrowed portion, the **spinal cord**. The **brain** is widest in front, and is dilated at intervals to form the **cerebral vesicles**, best seen from the side.

The **anterior cerebral vesicle**, or **forebrain**, **BF**, is still open in front: it is expanded laterally to form the **optic vesicles**, **OV**, of which the right one is exposed by removal of the surface epiblast. The second vesicle, or **mid-brain**, **MB**, is much smaller: and in the **hind-brain** the first of the series of vesicles of which it consists is alone shown.

The **notochord** is coloured green; and its anterior part, underlying the brain, is alone shown.

The **protovertebræ**, **PV**, are exposed on the right side: they are squarish blocks formed by transverse division of a longitudinal band of mesoblast, which at the hinder end of the embryo is still undivided.

The **fore-gut**, **GF**, is seen in section as a cavity extending forwards beneath the brain. It ends blindly in front, opposite the fore-brain; and its anterior wall is in close contact with the floor of the stomodeal depression, at the place where the mouth perforation will subsequently be formed.

The **pericardial cavity**, **PC**, lies below the fore-gut. Like the rest of the coelom, of which it is a part, the pericardial cavity lies between the body wall or **somatopleure**, and the gut wall or **splanchnopleure**; its anterior wall being formed by the somatopleure, and its roof, floor, and posterior wall by splanchnopleure. At

this stage the pericardial cavity consists of two separate cavities of which the one of the right side is opened in the model. The mesoblast lining the cavity is coloured pale red.

The **heart, H**, consists of two parallel tubes (compare models **4** and **18**), of which the right one (red) is seen through the mesoblast, receiving at its posterior end the right vitelline vein (red). In front, the heart leaves the pericardial cavity as the **first aortic arch** (red), which turns up round the side of the fore-gut, close to its anterior end, and then continues its course backwards as the **dorsal aorta** alongside the brain and protovertebræ. In the model the aorta stops at the point at which in the embryo the **vitelline artery** arises running outwards to the vascular area of the blastoderm to absorb food from the yolk.

The **amnion, AN**, is seen in section as a fold of the somatopleure in front of the embryo.

#### MODEL 6. Chick Embryo of about 33 hours.

##### DORSAL SURFACE.

The head of the embryo has greatly increased in size as compared with the earlier stage, model **3**, and is now folded off from the blastoderm by the head-fold as far back as the level of the ears.

The **neural canal** is closed in the head, and along the greater part of the length of the body, but at the hinder end of the embryo the neural folds are still a slight distance apart. In the head the outlines of the several brain vesicles and of the optic vesicles can be recognised through the external epiblast.

The **auditory vesicles, AV**, are a pair of deep pits at the sides of the hinder end of the brain.

Sixteen pairs of **protovertebræ** are present.

The head-fold of the **amnion, AN**, has grown considerably, and now forms a wall surrounding the head of the embryo, and extending back so as to cover over its anterior end.

##### VENTRAL SURFACE.

The lateral boundaries of the **mid-gut, GM**, are indicated by the outer pair of yellow lines. Owing to the increase in depth of the

head-fold, the entrance to the tunnel-like **fore-gut, GF**, is now considerably further back than in **Model 3**.

#### **MODEL 7. Chick Embryo of about 33 hours.**

The anterior part of the blastoderm has been removed so as to expose the head thoroughly and to show the amnion in section. The ventral wall of the pericardial cavity has also been removed to expose the heart.

For a general description of the model see **Model 6**.

#### **VENTRAL SURFACE.**

The **stomodæum**, or mouth invagination, **ST**, is the depression on the under surface of the head, in front of the cut edge of the blastoderm : it is more clearly defined and deeper than in the earlier stage (**Model 4**).

The **pericardial cavity** has been opened by removal of the splanchnopleure forming its ventral wall.

The **heart** (red), **H**, is a single tube, formed by coalescence of the two originally distinct halves (**Model 4**). It is attached to the ventral wall of the fore-gut both in front and behind : its middle portion is free, and, owing to its growing more rapidly than the rest of the embryo, is strongly looped : the convexity of the loop projecting towards the right side of the embryo.

The heart is formed behind by the union of the two **vitelline veins**, which are coloured red, and can be seen along the cut edge of the hinder border of the pericardium.

The side folds of the **amnion, AN**, are seen in section at the cut upper edge of the blastoderm, arising as upgrowths of the somatopleure.

#### **MODEL 8. Chick Embryo of about 33 hours.**

The external epiblast, and the whole of the nervous system, have been removed : as has also the greater part of the mesoblast, including the protovertebræ.

The parts shown in the model are the fore-gut, the heart, and the arterial and venous systems. The heart and arteries are coloured red, the vitelline veins and their branches grey.

For a general description of an embryo at this stage see **Model 6**.

## DORSAL SURFACE.

The **fore-gut, GF** (green), projects forwards in the model as a tongue-like process, embraced by the aortic arches (red). The lateral bulgings of the fore-gut between the aortic arches are the commencing gill pouches.

The network of blood-vessels (grey) at the sides of the anterior part of the model collects the blood from the vascular area of the blastoderm; the vessels of each side unite to form a **vitelline vein**, and the two vitelline veins unite beneath the fore-gut to form the heart.

The heart (red), **H**, forms a loop towards the right side (compare model **7**), and then returns to the under surface of the fore-gut, where it divides into two pairs of **aortic arches** (red). These embrace the sides of the fore-gut, and on its dorsal surface the two arches of each side unite to form the **dorsal aortæ**.

The two dorsal aortæ (red) run back side by side along the dorsal surface of the fore-gut and mid-gut. Posteriorly they diverge and run outwards as the **vitelline arteries**, which open into the meshwork of blood-vessels in the vascular area of the blastoderm, from which the vitelline veins arise further forward.

**MODEL 9. Chick Embryo of about 33 hours.**

The blastoderm of the right side has been removed by a longitudinal section along the side of the embryo: and the external epiblast has been removed from the right half of the embryo so as to expose the nervous system, the protovertebræ, and the heart and blood vessels.

For a general description of an embryo of this age see Model **6**.

The **brain and spinal cord** are white in the model. The anterior rounded end of the brain is formed by the **fore-brain, BF**, or anterior cerebral vesicle; from which the **optic vesicle, OV**, of the right side is seen arising as a lateral backwardly-directed bud. Behind the forebrain comes the **mid-brain, MB**, or middle cerebral vesicle, the limits of which are indicated by two transverse veins (blue). Behind the mid-brain is the **hind-brain, HB**, indistinctly divided by constrictions into vesicles, and extending back to the level of the first protovertebræ where it passes into the **spinal cord**, which can be followed to the hinder end of the embryo.

The **mesoblast** (red) of the body region is divided on either side by a longitudinal groove, well seen at the hinder end of the embryo, into **vertebral plate, VP**, lying alongside the spinal cord, and **lateral plate, LP**, more peripherally placed.

The **vertebral plate** is divided by transverse grooves into oblong masses, the **protovertebræ** or **myotomes** (dark red), of which fifteen pairs are present. Behind the fifteenth the vertebral plate is as yet unsegmented. The **lateral plate** of the mesoblast (pale red) is split horizontally into dorsal or **somatopleuric**, and ventral or **splanchnopleuric layers**. The space between these two layers, seen in the model as a deep longitudinal groove along the cut edge of the embryo, will form the body cavity, or **cœlom**, of the chick. It opens in front into the pericardial cavity.

Part of the lateral plate, about an inch in length in the model, has been removed from the hinder part of the embryo to expose the network formed by the vitelline blood-vessels (compare model 8.)

The **heart, H**, (pale red), is exposed by removal of the right wall of the pericardial cavity. The loop of the heart projects strongly towards the right side.

From the anterior end of the heart the two **aortic arches** (deep red) of the right side are seen arising: they run round the side of the fore-gut (green) and unite above this, and below the brain, to form the **dorsal aorta** of the right side, which runs backwards, lying ventral to the protovertebræ. (Compare model 8.) Of the two aortic arches the anterior one is the same as the single arch of the earlier stage (model 5): the posterior or second aortic arch, has developed since that stage.

Immediately behind the pericardium the cut end of the **right vitelline vein** (purple) is seen. The transverse vessel (purple) immediately above this is the **right Cuvierian vein**: this is formed by the union of the **anterior cardinal vein** (blue), which lies dorsal to the aorta and returns blood from the head, and especially from the brain; and the **posterior cardinal vein** (blue), which runs along the outer borders of the protovertebræ and returns to the heart the blood from the body of the embryo.

The head-fold of the **amnion, AN**, and its origin as a fold of the somatopleure, are well seen at the anterior end of the model.



**MODEL 10. Chick Embryo of about 48 hours.**

The embryo has been cut out from the blastoderm, and the amnion removed.

The head of the embryo, which in the earlier stages (see Model 6) lay with the ventral or facial surface downwards towards the yolk, is now twisted so as to lie with its left side downwards towards the yolk, and its right side upwards towards the egg shell. The body still retains the same relations as before, so that the axis of the embryo, previously a straight line, becomes twisted somewhat spirally.

**DORSAL SURFACE OF THE BODY AND RIGHT SIDE OF THE HEAD.**

The axis of the head is no longer straight, but, owing to the rapid growth of the dorsal surface, has become strongly curved on itself. By this **cranial flexure**, as it is called, the dorsal surface of the head is rendered strongly convex, and the anterior end of the brain bent over on to the ventral surface of the head.

Slight grooves on the surface of the head mark the division of the brain into regions, which are better seen in Model 11. The deep horizontal groove (brown) on the under surface of the fore part of the head is the mouth of the **olfactory pit, OL**; and the vertical groove meeting this at right angles marks the position of the lens of the eye. The deep pit immediately below the point of meeting of these two grooves, and on the under surface of the head, is the **stomodæum, or mouth invagination**.

The three deep grooves (red) crossing the neck are the three anterior visceral clefts, *i.e.*, in order from before backwards, the **hyomandibular cleft**, which is the largest of the three, the **first branchial cleft**, and the **second branchial cleft**. They place the pharynx in direct communication with the exterior.

The part of the neck in front of the hyomandibular cleft, between it and the stomodæum, is the **mandibular arch, MN**; the strip between the hyomandibular and first branchial clefts is the **hyoid arch, HY**; and the strip between the first and second branchial clefts is the **first branchial arch, BR 1**.

The circular depression above the dorsal end of the first branchial cleft is the mouth of the auditory vesicle.

In the body the neural canal is closed along its entire length ; and there are twenty-six pairs of protovertebræ present.

The **heart** is exposed by removal of the pericardial wall, but is more fully seen from the ventral surface.

#### VENTRAL SURFACE OF THE BODY AND LEFT SIDE OF THE HEAD.

The left side of the head is similar to the right side, already described : the stomodæal invagination is rather better seen. The **heart** (red) is a single tube attached both in front and behind to the under surface of the fore-gut, and with the middle portion of its length free and twisted on itself something like a letter **∞**. It is incompletely divided into chambers by transverse constrictions.

Commencing from the posterior end of the heart, the first or proximal limb of the **∞** is formed by the **sinus venosus, SV**, a wide, straight tube showing indications of its formation by fusion of the two vitelline veins. The sinus venosus opens in front into the **auricular portion, A**, from which the heart bends sharply towards the ventral surface and then across to the right side as the **ventricular portion, V**. It then bends sharply towards the dorsal surface as the distal limb of the **∞** or **truncus arteriosus, TA**, which runs forwards to the under surface of the fore-gut, reaching this at the level of the ventral ends of the visceral clefts, and a little way behind the stomodæum.

The **fore-gut** has greatly increased in length with growth of the embryo, but is not shown in this model (compare Models **11** and **22**). The **mid-gut, GM**, is the slightly depressed area on the ventral surface of the body, behind the heart : its boundaries are indicated by the groove tinted red. The posterior boundary, or tail-fold, is now fairly well defined.

At the edge of the blastoderm the cut ends of the **vitelline veins** (blue) and **vitelline arteries** (red) are shown.

#### MODEL 11. Chick Embryo of about 48 hours.

The external epiblast has been removed from the right side of the head and body, to expose the brain and the blood vessels. For a general description of an embryo of this age see Model **10**.

The **brain** (white) is bent round on itself, by the cranial flexure, through about  $180^{\circ}$ ; and so forms the anterior end and ventral surface of the head, as well as its dorsal surface. Of the several divisions of the brain, the **mid-brain, MB**, forms the anterior end of the head, and the uppermost part in the model: a forked branch of the internal carotid artery (red) lies on its side, and two branches of the anterior cardinal vein (blue) mark its anterior and posterior boundaries respectively. In front of the mid-brain is the **fore-brain, BF**, or **thalamencephalon**, the boundaries of which are indicated by veins (blue). Below the fore-brain is the **vesicle of the cerebral hemisphere, CH**, as yet unpaired; and on the side of this, embraced by two veins (blue), is the **optic vesicle**: this latter is doubled up on itself to form the **optic cup, OC**, the groove at the lower edge of which is the **choroidal fissure**.

The **hind-brain, HB**, lies behind the mid-brain, and separated from it by a marked constriction in which a vein (blue) lies. The deep cavity of the hind-brain, or **fourth ventricle**, has been exposed by removal of its thin roof. The pit (purple) at the hinder part of the hind-brain, just in front of the first protovertebra, and embraced by veins (blue) is the **auditory vesicle, AV**, or ear.

The anterior end of the **notochord** (green) is seen underlying the hind and mid brains.

The **fore-gut** (yellowish green) lies ventral to the hind-brain, and embraced by the heart and arteries (red): the forwardly directed conical diverticulum, in contact in front with the anterior end of the notochord below the base of the fore-brain, is the **pituitary body**, an outgrowth from the stomodæum.

The **heart, H** (red), has been already described in Model 10. On the right side two veins (purple) are seen entering the heart: of these the right hand one in the model, lying along the cut edge of the blastoderm, is the **right vitelline vein**, returning blood from the yolk sac. The left hand of the two veins is the **right Cuvierian vein** (purple), formed by the union of the **anterior cardinal vein** (blue) returning blood by numerous branches from the head, especially the brain; and the **posterior cardinal vein** (blue), returning blood from the body and running along the outer borders of the protovertebræ.

From the anterior end of the heart, or **truncus arteriosus, TA**, three complete **aortic arches** (red) arise, opening into the **dorsal aorta**, and an incomplete fourth arch which does not yet reach the aorta.

The anterior and longest of the three complete aortic arches is the anterior of the two present in Model 9, and the single one of Model 5: it lies in the mandibular arch. The second aortic arch lies in the hyoid arch; the third aortic arch in the first branchial arch; and the fourth aortic arch, as yet incomplete, in the second branchial arch.

From the anterior end of the dorsal aorta the **internal carotid artery** (red) runs forward along the brain, dividing into two branches on the side of the mid-brain.

The **dorsal aorta** is shown running back along the dorsal surface of the fore-gut, ventral to the anterior cardinal vein and to the protovertebrae. At the edge of the blastoderm the cut end of the **vitelline artery** (red) is seen, carrying blood from the aorta to the yolk sac.

Along the right side the **somatopleure** has been partly removed, a narrow strip alone being left along the outer side of the posterior cardinal vein. The **body-cavity** is seen as a longitudinal groove between the somatopleure and splanchnopleure.

**MODEL 12.** Chick Embryo of about the middle of the 4th day of incubation.

The embryo has been artificially straightened out. In the natural condition the head is bent down on the body much more strongly, the cerebral hemispheres lying opposite the rudiments of the fore-limbs.

#### THE HEAD AND NECK.

In the head the swellings caused by the several parts of the brain are very conspicuous. The prominent rounded swelling at the top of the head is caused by the **mid-brain, MB**: below this in front is the **fore-brain, BF**; and below this again forming the paired rounded projections at the front of the head, are the **cerebral hemispheres, CH**. The horizontal groove (brown) on the side of the hemisphere is the mouth of the **olfactory pit, OL**, which is prolonged backwards as the **nasal groove** to the mouth.

The **eye, OC**, lies at the side of the fore-brain, and between the mid-brain and the cerebral hemisphere. The spherical body (green) in its centre is the **lens**. The upper part of the oblique groove running from the lens to the mouth is the **choroidal fissure**; the lower part is the **lachrymal groove**, the distinctness of which is somewhat exaggerated in the model.

Behind the mid-brain, and forming the dorsal region of the hinder part of the head, is the **hind-brain, HB**. Its thin roof is coloured bluish-white.

At the side of the neck the four **gill clefts** are indicated by deep grooves, coloured red: the most anterior and longest of the four is the **hyomandibular cleft**; the second, third, and fourth are the **first, second, and third branchial clefts** respectively.

The small pit above the dorsal ends of the hyomandibular and first branchial clefts indicates the position of the **auditory vesicle, AV**, the mouth of which is, however, closed at this stage.

The **stomodæum** is the deep depression on the under surface of the head, towards which the nasal and lachrymal grooves converge. It is pentagonal in outline, and is bounded behind by the ventral ends of the **mandibular arches, MN**; at the sides by the **maxillary arches, MX**, the upper limits of which are indicated by shallow grooves on the sides of the head; and in front by the **fronto-nasal process**, formed by the under surface of the anterior end of the head.

#### THE BODY.

The longitudinal axis of the body is twisted spirally; the head and interior part of the body lying with their left side downwards and resting on the yolk sac, while in the posterior part of the body the ventral surface is still directed downwards.

The **protovertebræ**, of which there are now 41 pairs, are clearly seen through the external epiblast, extending along the entire length of the body and almost to the tip of the tail. The longitudinal ridge running along the whole length of the body on each side, ventral to the protovertebræ, and separated from them by a groove, is the **Wolffian ridge, WR**. At two places, opposite the vitelline veins, and opposite the tail, the ridges are more prominent, forming the rudiments of the **wings, W**, and **legs, L**.



The **heart** (red) forms a conspicuous loop, projecting from the ventral surface of the body behind the head. It is attached at its two ends to the ventral surface of the fore-gut, and is free along the rest of its length. The **sinus venosus** is the most posterior part of the heart, into which the vitelline veins (purple) open. The **auricular portion, A**, comes next, the lateral bulgings caused by the right and left auricular appendices being well shown. The **ventricular portion, V**, forms the most prominent part of the loop ; it is separated by a slight constriction from the **truncus arteriosus, TA**, which forms the distal and longest limb of the loop, returning to the ventral wall of the fore-gut opposite to the gill clefts.

The cut ends of the **vitelline arteries** (red) are seen at the edge of the model about an inch behind the vitelline veins.

Of the **alimentary canal** the **mid-gut** and **hind-gut** are shown in the model.

The **mid-gut** is the deep longitudinal groove on the ventral surface of the body ; its walls are formed by the splanchnopleure. The deepest part of the groove at the anterior end, between the vitelline veins, will become the **stomach**. The two lateral depressions (green) opposite the cut ends of the vitelline veins are the rudiments of the **liver, R**. The slightly twisted part between the liver rudiments is the **duodenum**.

The **hind-gut** is the pocket-like cavity into which the mid-gut opens posteriorly : the longitudinal groove on its ventral wall is the commencing **allantois, AL**.

**MODEL 13. Chick Embryo of about the middle of the fourth day.**

For a general description of an embryo of this age see Model 12. The body wall of the right side is removed to expose the brain, spinal cord, alimentary canal, and blood-vessels.

The **nervous system** is shown white. The **cerebral hemispheres, CH**, are the pair of prominent lateral swellings at the extreme anterior end of the brain. The **fore-brain, or thalamencephalon, BF**, is the part above and behind the hemispheres, from which the latter arise. The **optic cup, OC**, lies on the side of the fore-brain, behind the cerebral hemispheres : the groove

interrupting its lower margin is the **choroidal fissure**. The **lens** is removed from the eye of the right side, but is present in the left eye. The **mid-brain, MB**, is the prominent rounded swelling, forming, in the model, the uppermost part of the brain: branches of the internal carotid artery (red) lie on its side: and branches of the anterior cardinal vein (blue) lie in the grooves separating it from the fore-brain and mid-brain respectively. The **cerebellum, C**, is the curved roof of the front of the hind-brain, immediately behind the mid-brain. The rest of the **hind-brain**, extending back to the level of the first protovertebra, is the **medulla oblongata, MO**: the deep spoon-shaped pit on its dorsal surface is the **fourth ventricle**, which is exposed in the model by removal of its thin roof (compare Model 12). The **spinal cord** is directly continuous with the hind-brain, and may be traced to the extremity of the tail.

The **auditory vesicle, AV**, (purple) lies at the side of the medulla, closely embraced by branches (blue) of the anterior cardinal vein.

The **notochord** (green) is a cylindrical rod lying immediately ventral to the spinal cord and brain. It extends to the extreme hinder end of the tail, and anteriorly it stops beneath the hinder part of the fore-brain.

The **heart** (red) **H**, forms a somewhat spiral loop projecting prominently from the ventral surface of the embryo: it has been fully described in Model 12.

On the right side of the model, two veins (purple) are shown opening into the sinus venosus or proximal end of the heart. One of these, the **vitelline vein** (purple), returning blood from the yolk sac, runs vertically along the border of the splanchnopleure close to its cut edge. The other, or **Cuvierian vein** (purple), enters the sinus venosus horizontally: it is formed by the union of the **anterior cardinal vein** (blue) returning blood by numerous branches from the head, and especially from the brain, eye, and ear; and the **posterior cardinal vein** (blue), a longitudinal vessel returning blood from the hinder part of the body, and lying parallel to the spinal cord and a little way ventral to it.

Arising from the **truncus arteriosus**, or distal end of the heart, are five pairs of **aortic arches** (red), best shown on the right side of

the model. The most anterior, or **first aortic arch**, lying in the mandibular arch, is incomplete, its connection with the dorsal aorta (compare models **5**, **9** and **11**) being lost. The **second, third, and fourth aortic arches**, lying in the hyoidean, first branchial and second branchial arches respectively, are complete, reaching and opening into the dorsal aorta. The **fifth aortic arch**, in the third branchial arch, is just commencing to form, and is as yet a very short, blind process from the truncus arteriosus.

The **internal carotid artery** (red) is an anterior continuation of the dorsal aorta, and runs forward alongside the notochord, ending in branches to the mid-brain, forebrain and eye.

The **dorsal aorta** (red) runs down the back of the embryo, immediately ventral to the notochord. About the middle of its course it gives off the **vitelline artery** (red), which runs outwards in the splanchnopleure, and is seen in section at the cut edge of the mid-gut.

The **fore-gut** (greenish yellow), **GF**, is exposed along its whole length on the right side by removal of the body wall. Its anterior part is encircled by the aortic arches between which are the pouch-like outgrowths which form the gill clefts. In front the fore-gut opens at the **stomodæal** or **mouth aperture**, from which the **pituitary body**, **PB**, runs forward as a conical diverticulum, meeting the anterior end of the notochord beneath the fore-brain.

The **Wolffian tubules**, forming the embryonic kidney, are represented in the model as a series of squarish masses (brown), really convoluted tubes, lying along the hinder part of the body, and connected with the **Wolffian duct** (brown), a longitudinal tube lying alongside and ventral to the posterior cardinal vein, and opening behind into the hind-gut.

**MODEL 14. The Brain of a Chick Embryo of about 29 hours.**

For descriptions of embryos of this age compare Models **3**, **4**, and **5**.

The axis of the brain is nearly straight, the anterior end being slightly bent towards the ventral surface by the commencing **cranial flexure**.

The anterior enlarged end is the **fore-brain, BF**; its lateral expansions are the **optic vesicles, OV**; and the median prolongation forming the extreme end of the brain is the unpaired **vesicle of the hemispheres, or cerebral vesicle, CH**.

Behind the fore-brain, and separated from it by a slight constriction, is the **mid-brain, MB**; behind which is the **hind-brain, HB**, forming the rest of the model.

**MODEL 15. The Brain of a Chick Embryo of about 33 hours.**

For descriptions of embryos of this age compare Models **6, 7, 8** and **9**. Owing to the cranial flexure the axis of the brain is distinctly curved; the dorsal surface of the brain being convex, the ventral concave.

The **fore-brain, BF**, with the **vesicle of the hemispheres, CH**, forms the enlarged anterior end of the brain, from which the **optic vesicles, OV**, arise as a pair of lateral, backwardly directed outgrowths. The projection on the under surface of the floor of the fore-brain is the **infundibulum, IN**.

The **mid-brain, MB**, is the globular vesicle behind the fore-brain, marked by the number 15; it is separated by a constriction from the **hind-brain, HB**, which shows more or less clear indications of division into a series of vesicles.

**MODEL 16. The Brain of a Chick Embryo of about 48 hours.**

For descriptions of embryos of this age compare Models **10** and **11**.

Cranial flexure is strongly marked, the brain being bent round through more than  $180^{\circ}$

The **mid-brain, MB**, forms the uppermost part in the model: it is separated by a marked constriction from the hind-brain, and by a less evident one from the fore-brain.

The **fore-brain, BF**, and the **vesicle of the hemispheres, CH**, form the anterior part of the brain. At the sides of the fore-brain are the **optic vesicles**, doubled-up on themselves to form the **optic cups, OC**: the lip of each optic cup is interrupted below by the **choroidal fissure**. The projection on the ventral surface of

the fore-brain, opposite the optic cup, is the **infundibulum**; and the projection on the dorsal surface of the fore-brain, opposite the infundibulum, marks the position of the **pineal body**.

The cavity of the hind-brain, or **fourth ventricle**, has been exposed by removal of its thin roof. The thickened ridge, forming the upper or anterior boundary of the ventricle, just behind the constriction between hind-brain and mid-brain, is the **cerebellum**.

**MODEL 17. The Brain of a Chick Embryo of about the middle of the fourth day.**

For descriptions of embryos of this age compare Models **12** and **13**.

Cranial flexure, though really as strongly marked, is not quite so conspicuous as in Model **16**, owing to the outgrowth of the paired cerebral hemispheres at the anterior end of the brain.

The **fore-brain, BF**, is of large size, and forms the anterior part of the brain: from it the **cerebral hemispheres, CH**, arise in front as lateral outgrowths: these are directed upwards and forwards, and cause the apparent diminution in cranial flexure seen on comparison with Model **16**. The **optic vesicles** arise from the sides of the fore-brain behind the hemispheres; they are completely doubled up to form the **optic cups, OC**, the lower margins of which are interrupted by the **choroidal fissures**. Below and behind the optic cups the floor of the fore-brain is produced downwards to form the **infundibulum, IN**.

The **mid-brain, MB**, lies behind the fore-brain, and forms the uppermost part in the model: it is separated by well-marked constrictions from both fore-brain and hind-brain.

In the **hind-brain, HB**, the anterior part of the roof forms a thick crescentic band, the **cerebellum**. The rest of the hind-brain is the **medulla oblongata**, of which the cavity, or **fourth ventricle**, has been exposed in the model by removal of its thin roof.

**MODEL 18. The Heart of a Chick Embryo of about 29 hours.**

For descriptions of embryos of this age compare Models **3**, **4**, and **5**.



The **heart, H** (dark red), consists of two parallel tubes, lying side by side and coalescing anteriorly.

The **pericardial cavity, PC** (pale red), consists of two halves, right and left, completely separate from each other: the line of meeting of the two halves is indicated on the ventral surface by a longitudinal groove.

**MODEL 19. The Heart of a Chick Embryo of about 33 hours.**

For descriptions of embryos of this age compare Models **6, 7, 8** and **9**.

The **heart, H**, is a tube bent into a **C** shaped loop: it is attached at its ends to the wall of the pericardial cavity (pale red), but is free in the middle part of its length, which forms a loop projecting towards the right side of the embryo.

The lower or posterior end of the loop receives the two **vitelline veins**, while from the upper or anterior limb, the **aortic arches** arise.

**MODEL 20. The Heart of a Chick Embryo of about 48 hours.**

For descriptions of embryos of this age compare Models **10** and **11**.

The **heart** is a single tube, twisted on itself like a letter **∞**. The proximal end of the heart, or **sinus venosus, SV**, is wide and receives the vitelline and Cuvierian veins (compare Model **11**): it opens into the **auricular portion, A**, which already show signs of division into right and left auricles. The succeeding, or horizontal limb, is the **ventricular portion, V**; and the final, anteriorly directed, and longest limb is the **truncus arteriosus, TA**.

**MODEL 21. The Heart of a Chick Embryo of about the middle of the fourth day.**

For descriptions of embryos of this age compare Models **12** and **13**.

The **heart**, as in Model **20**, is twisted in an **∞** shaped loop. The proximal end, or **sinus venosus, SV**, receives the vitelline veins below, and the **Cuvierian veins** laterally. It opens into the **auricular portion, A**, in which the division into right and left auricles is clearly seen. The succeeding part is the **ventricular**

portion, **V**, the number **21** marking the future apex of the ventricles. The terminal, anteriorly directed and longest limb is the **truncus arteriosus**, **TA**, in the cut end of which are seen indications of the division into **aortic arches**. (Compare Model **13**).

**MODEL 22. The Alimentary Canal of a Chick Embryo of about 48 hours.**

For descriptions of embryos of this age compare Models **10** and **11**.

The alimentary canal consists of an anterior part or **fore-gut**, which is tubular ; and a posterior part, or **mid-gut**, which is widely open to the yolk.

**Fore-gut.** The conical prolongation at the extreme anterior end is the **pituitary body**. At its base on the ventral surface is the oval **stomodæal**, or **mouth opening**, **ST**, leading into the pharynx. The three pairs of pouch-like outgrowths from the sides of the pharynx are the **hyomandibular**, **HM**; **first branchial**, **B.1**; and **second branchial**, **B.2**; gill pouches respectively. Behind the gill pouches the fore-gut narrows to form the **œsophagus**, **O**.

**Mid-gut.** The ventral service of the mid-gut is marked by a shallow median groove (red) ; and by two lateral grooves (red) which indicate the boundaries of the lateral margin of the gut. The green patches, **HH**, mark the places where the liver outgrowths will arise at a slightly later stage.

The transverse groove (red) at the hinder end, just in front of the figures **22**, indicates the commencing **tail fold** by which the hind-gut will become folded off.

**MODEL 23. The Alimentary Canal of a Chick Embryo about the middle of the fourth day.**

For descriptions of embryos of this age compare Models **12** and **13**.

The alimentary canal consists now of three lengths ; an anterior part, or **fore-gut**, which is tubular, and forms nearly half of the entire length ; a middle region, or **mid-gut**, of about equal length, which is a deep longitudinal groove with roof and sides but no floor ; and a short posterior region, or **hind-gut**, in the form of a deep pocket at the hinder end of the embryo, the floor of which is formed by the tail fold.

**Fore-gut.** The anterior pointed process, forming the uppermost part of the model is the **pituitary body, PT**; below this, on the ventral surface, is the **stomodæal opening**, or mouth, a lozenge-shaped aperture bounded posteriorly by the **mandibular arches, MN**, which meet at the chin, and anteriorly by the **maxillary processes, MX**, the rudiments of the upper jaw. The paired sacculations behind the mouth are the gill pouches. The brown coloured swelling, **P**, on the ventral surface of the hinder end of the fore-gut, is formed by the rudiments of the **lungs**.

The dorsal wall of the fore-gut has been removed to expose its cavity. In front the **gill pouches** are seen as lateral foldings of the wall of the pharynx. The median longitudinal groove, **T**, along the floor of the pharynx is the **thyroid groove**, and the two lateral pouches at the posterior end of the fore-gut are the **lungs**.

**Mid-gut.** The deep groove, **S**, at the anterior end, immediately behind the fore-gut, is the **stomach**. The lateral depressions, **HH**, (green) are the commencing **liver** diverticula. The pit, **P**, in the right wall of the mid-gut, immediately behind the liver, is the commencing **pancreas**; and the longitudinal groove behind it, **I**, is the **intestine**. The thin vertical fold along the dorsal surface of the mid-gut, lettered in front, **L**, is the **mesentery** attaching the alimentary canal to the dorsal body wall.

**Hind-gut.** The left hand wall of the hind-gut is removed to expose its cavity. The **allantois, All**, is seen arising as an outgrowth from its ventral wall.

## PREFACE.

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THE only important addition to the text in this edition of the Catalogue is the description of the models illustrating the development of Torpedo. The original descriptions of the other models were so clear and concise that it was not found necessary to make more than a few minor alterations. The recent investigations of MacBride on the development of Amphioxus and Asterina have, however, shown that the models of these series are in certain respects incorrect, and I have been obliged to add some notes to the descriptions of them to indicate to the student the principal points upon which new light has been thrown.

S. J. H.

*November 3rd, 1902.*

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## Description of a Series of Wax Models illustrating the Early Development of the DOG.



### CASE VI.

*The Models are by Dr. Ziegler, from the figures and descriptions of  
Professor Bischoff.\**

The dog is developed from an **ovum** or egg, Model **2**, which measures about 0.16 mm. in diameter. On its discharge from the ovary the ovum is received into the open mouth of the Fallopian tube or oviduct, a narrow tube about four inches in length, opening below into the uterus. The ovum passes quickly along the first part of the oviduct, but remains for some days in the lower end, where it is fertilised, and passes through the several stages of segmentation, (Models **2** to **6**).

From eight to ten days after its discharge from the ovary the ovum enters the uterus, in which the remainder of the development is effected. Development proceeds for a time very slowly : and the first trace of the embryo, Model **12**, does not appear until the middle or the end of the third week from the time the ovum left the ovary. From this time development goes on much more rapidly, and at the end of the ninth week after discharge of the ovum from the ovary the young puppy is born.

After entering the uterus the ovum lies for a time quite freely within it : it soon, however, becomes fixed to the wall of the uterus by means of the **placenta**, an organ in which the blood vessels of the embryo

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\* Bischoff, "Entwicklungsgeschichte des Hunde-Eies" ; Braunschweig, 1845.

and of the mother come into close and intricate relation with one another, and the blood of the embryo is able to take up nutrient matters from that of the mother. It is in consequence of the supply of food obtained in this way that the young mammal, though developed from an extremely small egg, is able to attain so great a size at the time of birth.

The models illustrate the stages of development passed through during the first three weeks. Models **1** to **9**, illustrating the earliest stages, are 100 times the linear dimensions of the natural objects. Models **10** to **14**, which show the first appearance of the embryo and the stages immediately preceding this, are 10 times the linear dimensions of the natural objects.

It is impossible to determine with certainty the ages of dog embryos, owing to the doubt as to the actual time at which the ovum leaves the ovary and is fertilised: there appears also to be considerable variability in the rate of development in individual cases, especially in the earlier stages. The ages given in the following descriptions are in accordance with Bischoff's determinations.

**MODEL 1.** Ripe egg, enclosed in the **zona pellucida** or **vitelline membrane**. x 100. /

**MODEL 2.** Ripe egg, with one-half of the **zona pellucida** (white), removed to expose the **ovum** (yellow). The **ovum** is a single cell, consisting of a spherical mass of protoplasm, about 0.16 mm. in diameter, in which are imbedded a number of minute **yolk granules** to which the opacity of the ovum is due. Within the protoplasm is also the **nucleus** or **germinal vesicle**, not seen in the model, a small spherical capsule about 0.04 mm. in diameter, filled with fluid in which lie one or more **nucleoli** or **germinal spots**.

The **zona pellucida** or **vitelline membrane** is a transparent, elastic investment about 0.02 mm thick. To it the spherical shape of the egg is due; and if it be punctured, the semi-fluid protoplasm of the egg at once pours out.

Models **1** and **2** represent the condition in which the ovum leaves the ovary and enters the oviduct. In the natural condition the ovum is usually invested by an irregular layer of cells derived from the Graafian follicle; but these play no part in development, and gradually

get rubbed off as the ovum travels down the oviduct, or after it enters the uterus. × 100.

**MODEL 3. Ovum** from the lower end of the oviduct, showing the first stage of **segmentation**. Half the vitelline membrane has been removed to expose the ovum, which has divided into two cells of equal size. × 100.

**MODEL 4. Ovum** from the lower end of the oviduct, about  $\frac{1}{2}$  inch from the entrance to the uterus. The egg has now divided into four cells approximately equal in size. × 100.

**MODEL 5. Ovum** from the lower end of the oviduct, about  $\frac{1}{6}$  inch from the entrance to the uterus. At this stage, which is twenty-four hours later than that of model 4, the egg has divided into eight cells. × 100.

**MODEL 6. Ovum** from the lower end of the oviduct, close to the entrance to the uterus. The ovum has divided into eighteen cells, some of which are distinctly larger than others. × 100.

**MODEL 7. Ovum** just after its entrance into the uterus; *i.e.*, from eight to ten days after its discharge from the ovary. By further division the cells have become smaller and more numerous. The whole ovum has increased slightly in size; and a cavity, filled with fluid, is present in its interior. × 100.

**MODEL 8. Ovum** at a slightly later stage. The cells have increased in number, and are now arranged in a regular manner on the surface. × 100.

**MODEL 9. Ovum** at a rather later stage. As in models 1 to 8, half the **zona pellucida** (white) has been removed to expose the ovum. The ovum has increased considerably in size, and is now about double its original diameter. It is, however, not solid, but a hollow vesicle filled with fluid. The structure of the wall has not been made out accurately, and no attempt is made to show it in the model: it appears to consist of a single layer of cells over the greater part of its extent, but with a second or inner layer forming a thickened patch on one side. To the hollow ovum of this and the succeeding stages the name **blastodermic vesicle** is given. × 100.

**MODELS 10 to 14.** The models 10 to 14 illustrate the stages of development that occur towards the end of the third week. The

changes shown by these five models do not occupy more than a couple of days ; but between the stage shown in model **9** and that of model **10** there is an interval of about a week. The changes that occur during this week are very imperfectly known in the dog. From what is known to occur in other animals, it is probable that they consist chiefly in a steady increase in size of the hollow ovum, or **blastodermic vesicle** as it is now termed, which, while still lying quite free within the uterus, attains by the stage shown in model **10** a diameter more than twenty times that of the original ovum. At the same time, by spreading at its margins the inner layer of cells grows round the interior of the vesicle, and the wall of the vesicle thus consists of two layers of cells throughout its whole extent. These stages are well illustrated by the three models showing the development of the rabbit's blastodermic vesicle. (pp. 55-57.)

In comparing the models it must be remembered that while Models **1** to **9** are 100 times, Models **10** to **14** are only 10 times the dimensions of the natural objects. Model **10**, for example, if made to the same scale as Model **9**, would be about eighteen inches in diameter.

The **zona pellucida** (white) in Models **10** to **13** has been removed from a circular patch in the middle of the model so as to expose the wall of the blastodermic vesicle (blue) beneath it. In Model **14** the **zona pellucida** has been removed completely.

**MODEL 10.** The upper half of an ovum, or **blastodermic vesicle**, of about the middle of the third week. The vesicle, which is spherical, measures in the natural condition about four mm. in diameter. It lies quite freely in the uterus, and is still invested by the **zona pellucida**. In the model the **zona pellucida** (white) is left *in situ* round the margin, but has been removed from a circular patch in the centre so as to expose the blastodermic vesicle. The wall of the blastodermic vesicle is double, consisting of two layers, each composed of flattened epithelial cells fitted together edge to edge. The outer layer, or **epiblast** (blue), is exposed in the centre of the model by removal of the **zona pellucida**, and is also seen at the cut edge of the opposite side of the model. The inner layer, or **hypoblast** (yellow), lines the whole of the interior of the vesicle.

In the centre of the outer surface of the vesicle is a thickened and slightly raised patch (white), circular in outline. This is the **embryonal area**, and in its centre the first trace of the embryo will appear at a slightly later stage. It consists of the same two layers, epiblast and hypoblast, as the rest of the vesicle ; and its prominence is due to a great increase in the thickness of the epiblast at this part. × 10

**MODEL 11.** The upper half of a **blastodermic vesicle** at a slightly later stage than Model 10. The entire vesicle has increased in size, and is now somewhat ovoidal in shape. Its structure is the same as in Model 10, except that the **embryonal area** is rather larger, and oval in place of circular in outline. × 10

**MODEL 12.** The upper half of a **blastodermic vesicle** towards the ends of the third week. As compared with Model 11 there is a further increase in size of the entire vesicle, and also a considerable increase in the size of the embryonal area (white), which is now distinctly pyriform in outline, measuring in the natural object two mm. in length by one mm. in width at its widest part. The wider end corresponds to the anterior or head end of the embryo, the narrower end to its posterior or tail end. In the median line, and extending along the posterior two-thirds of the length of the embryonal area, is a longitudinal furrow, the **primitive groove** ; it corresponds exactly in mode of formation, in structure, and in relations with the primitive groove of the chick embryo ; and like this, though immediately preceding the embryo in time of appearance, it does not give rise directly to any of its organs. × 10

**MODEL 13.** The upper part of a **blastodermic vesicle**, about six hours later than that of Model 12. The entire blastodermic vesicle is at this stage a thin walled sac, shaped much like a lemon, and measuring about seven mm. in length by six mm. in width. It lies in the uterus with its longer diameter corresponding with the axis of the uterus ; and it adheres slightly to the wall of the uterus by tag-like processes from the zona pellucida, which penetrate into the mouths of the uterine glands.

The part represented in the model is the central portion of the upper wall of the vesicle. As compared with Model 12 the



**embryonal area** (white) has increased in size : it is still pyriform in outline ; and its main axis is at right angles to that of the entire blastodermic vesicle : *i.e.*, the axis of the embryonal area, which coincides with the axis of the embryo, is directed across the uterus, not along it.

A median longitudinal groove runs almost the whole length of the embryonal area. This really consists of two parts, the distinction between which is not clearly shown in the model. The posterior half, or rather more, of the groove is the **primitive groove**, and corresponds to the entire length of the groove in Model 12. The anterior part of the groove, opposite the widest part of the embryonal area, is wider and deeper than the primitive groove, and is the commencing **neural groove**. This gives rise later on to the brain and spinal cord of the young dog : it is the first of the organs to be definitely established, and its appearance marks the first stage in the formation of the embryo. × 10

**MODEL 14.** The upper part of a **blastodermic vesicle**, six hours earlier than that of Model 13, and twelve hours older than that of Model 12. As already noted, it is difficult or impossible to determine the precise age of dog embryos, owing to the uncertainty as to the time at which the ovum leaves the ovary and development commences. Bischoff estimates the embryo of Model 14 at about the end of the third week.

The entire **blastodermic vesicle** measures at this stage about nine mm. by five mm., and is shaped like a lemon, with rather pointed ends. The model, like the previous ones, represents the central portion alone of the upper wall of the vesicle.

The **embryonic area** has increased greatly in length ; it is shaped like a finger biscuit, wider at the ends, and slightly constricted in the middle. The deep groove running along its entire length, represents, as in Model 14, two really independent structures ; the posterior and narrower part, about  $\frac{2}{3}$  of the entire length, being the **primitive groove**, which is still the same length as in Model 12 ; while the anterior  $\frac{1}{3}$  is the **neural groove**, which has now greatly increased in length.

The lips of the neural groove are considerably thickened ; and the outline of the embryo (white) is defined by a groove separating it from the wall of the vesicle (blue).

The stage shown for the dog in Model **14**, corresponds very closely with that of Model **1** in the series illustrating the development of the chick ; and the actual sizes of the two embryos at this stage are practically identical.

From this point the development of the dog embryo proceeds rapidly, and in almost exactly the same way as the chick. In about twelve hours from the stage shown in Model **14** the several divisions of the brain are well established, the head is folded off from the wall of the blastodermic vesicle and the dog embryo has reached a stage corresponding to that of a chick embryo at the end of the first twenty-four hours of incubation.

Twelve hours later still, *i.e.*, twenty-four hours after the stage shown in Model **14**, the lips of the neural canal have met and fused, so as to give the central nervous system its definite tubular character, except at the extreme anterior end of the brain and the hinder end of the spinal cord. Rudiments of the eyes and ears are present ; ten pairs of protovertebræ are already developed ; and the heart is a tube, twisted on itself like a letter **S**. The stage reached corresponds almost exactly to that of a chick embryo at the thirty-third hour of incubation. (Compare Models **3**, **4**, and **5** of the series illustrating the development of the chick).

× 10

## Description of three Models illustrating certain stages in the Development of the RABBIT.



### CASE IX.

*The models are by Dr. Ziegler, from the figures and descriptions of  
Professor Bischoff.\**

The rabbit is developed from an ovum or egg measuring about 0.12 mm. in diameter, *i.e.*, slightly larger than the ovum of Amphioxus, and a little smaller than that of the dog. The general history of development is very similar to that of the dog, though the total time occupied, thirty days, is less than half that of the dog. The egg after discharge from the ovary takes three days to travel down the oviduct, during which it passes through the stages of segmentation, corresponding closely to those shown in models 1 to 7 of the series illustrating the development of the dog.

On entering the uterus at the end of the third day it is a solid ball about 0.09 mm. in diameter, *i.e.*, rather smaller than the original ovum, and consisting of an outer layer of rather smaller cells enclosing a central mass of rather larger and more granular cells.

Within the uterus the ball rapidly increases in size. The outer layer of cells grows much faster than the central mass; and by the end of the fourth day the ovum is a hollow ball about 0.3 mm. in diameter,

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\* Bischoff, "Entwicklungsgeschichte des Kaninchen-Eies," Braunschweig, 1842;  
Marshall, "Vertebrate Embryology," p. 341-447, London, 1893.

its wall consisting of a single layer of flattened cells formed from the outer layer of the earlier stage, while the original inner or central cells form a circular patch, thicker in the middle and thinning towards the edge, adhering to the inner surface of the ball at one spot. The rest of the cavity of the ball is filled with fluid.

In the following days the ball, or **blastodermic vesicle**, as it is now termed, continues to grow rapidly ; on the fifth day it is 1·5 mm. in diameter ; on the sixth day 3 mm., and on the seventh day 4 to 5 mm. At the same time changes are taking place in its walls : the circular thickened patch where both inner and outer cells were present on the fourth day becomes the **embryonal area**, and in the middle of this area during the eighth day the first trace of the embryo appears, exactly in the way shown in models **11** to **14** of the series illustrating the development of the dog.

The three models of the present series illustrate the changes that occur in the blastodermic vesicle of the rabbit during the sixth and seventh days, *i.e.*, the period during which the two primary germinal layers **epiblast** and **hypoblast** are being definitely established, immediately before the first appearance of the embryo.

In all three models the blastodermic vesicle is represented bisected vertically ; one-half alone being shown. The **embryonal area** is at the top of the model in each case, and the colours employed have the following significance :

**White** :—Zona pellucida or vitelline membrane :

**Blue** :—Epiblast :

**Yellow** :—Hypoblast :

**MODEL 1.** Blastodermic vesicle of a Rabbit towards the end of the sixth day.

The outermost layer in the model is the **zona pellucida** or **vitelline membrane** (white).

The wall of the blastodermic vesicle itself consists of a single layer of **epiblast** cells (blue), except in the **embryonal area** at the top of the model, where there is, in addition, an inner layer of **hypoblast** cells (yellow). The epiblast of the embryonal area is much thicker than that of the rest of the vesicle.

The condition shown in the model is derived from that of the fourth day, described on p. 55, in the following manner:—The circular patch of inner cells of the fourth day splits into two layers, upper and lower: of these the upper layer becomes the epiblast of the embryonal area of the model, and the lower layer the hypoblast. The thin epiblastic wall of the rest of the vesicle is derived directly from the outer cells of the fourth day, which originally cover the embryonal area as well, but disappear from this during the sixth day.

Both layers—epiblast and hypoblast—of the embryonal area are thus derived from the inner cells of the fourth day, while the epiblast of the rest of the vesicle is formed from the outer cells of the fourth day.

× 10

**MODEL 2. Blastodermic vesicle of a Rabbit towards the end of the seventh day.**

The whole vesicle has increased in size. The **hypoblast** (yellow), which was previously confined to the embryonal area, has now spread, by growth at its margin, so as to line the upper half of the vesicle. At this stage, therefore, the lower half or hemisphere of the blastodermic vesicle consists of a single layer of cells, **epiblast**, alone; the upper half or hemisphere consists of two layers of cells, **epiblast** and **hypoblast**; and in the centre of the upper half is the **embryonal area**, characterised by the greater thickness of the epiblast cells, which are here columnar in shape, while over the rest of the vesicle they are flattened.

× 9

**MODEL 3. Blastodermic vesicle of a Rabbit during the earlier part of the eighth day.**

The blastodermic vesicle has increased further in size, and is usually somewhat ovoidal in shape. Up to this time it has been lying quite freely in the uterus, but it now begins to acquire attachment to its walls.

The **hypoblast** (yellow), has spread so as to form a complete lining to the vesicle, the walls of which consist at this stage of two layers of cells, **epiblast** and **hypoblast**, at all parts. The **embryonal area**, which is now pyriform instead of circular in



shape, differs from the rest of the vesicle merely in the greater thickness of its epiblast, due to the columnar shape of its individual cells.

A few hours later than the stage shown in the model the **primitive streak** is formed, and a few hours later still the first indication of the embryo appears as the **neural groove**: the mode of development of these structures is practically the same in the Rabbit as in the Dog, and will be readily understood from a comparison of Models **11** to **14** of the series illustrating the development of the dog (Case VI).

× 8

# Description of a Series of Wax Models illustrating the Early Stages in the Development of the HUMAN EMBRYO.

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## CASE III.

*The Models are by Dr. Ziegler, from the drawings and descriptions of Professor His.\**

*Models 1 to 5 are forty times, and Models 6 to 8 twenty times the linear dimensions of the natural objects.*

*The actual dimensions given are in each case the greatest length of the embryo, measured in a straight line : i.e., the longest straight line that can be drawn through the embryo. In Models 1 to 5 this corresponds approximately to the longitudinal axis of the embryo : in Models 6 to 8 it is a line running from about the junction of the head and neck to the sacral region, opposite the hind limbs.*

The human embryo is developed from an ovum which measures 0.2 mm. in diameter ; i.e., is about twice the diameter of the ovum of *Amphioxus* and about a tenth of that of the frog's ovum. The segmentation of the human ovum, which probably takes place while it is travelling down the Fallopian tube towards the uterus, has not yet been seen : and our knowledge of the stages earlier than that shown in Model 1 is exceedingly imperfect.

The models illustrate the development of the human embryo during a period of about a fortnight : from the end of the second week to the

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\* His, "Anatomie menschlicher Embryonen," 1880-1885 ; Marshall, "Vertebrate Embryology," p. 448-619, London, 1893.

end of the fourth week. The ages given are probably correct within narrow limits, but must not be regarded as precisely determined, as it is seldom possible to fix the exact age of an embryo.

Professor His has given careful descriptions and figures of nearly all the known specimens of early human embryos, and has distinguished them by the letters quoted below.

**MODEL 1. Embryo lettered by Professor His, *R.S.*, and estimated as about 13 days old.**

Greatest length of embryo 2·2 mm.

The **embryo, E** (light brown), is very slightly constricted off from the large **yolk sac, Y** (yellow). The dorsal surface of the embryo is occupied by the **neural plate** (white), along the middle of which runs the **neural groove**, bordered by the **neural folds, NF**, which have not yet met at any part of their length.

The dorsal surface is not straight, but sinuous, presenting alternate convexities and concavities: the most anterior swelling, uppermost in the model, marks the head; then comes a concavity, indicating the neck, or cervical region, behind which are a convex thoracic, a concave lumbar, and a convex caudal region.

The white line at the boundary between the embryo and the yolk sac indicates the cut edge of the **amnion**, which forms a thin membrane covering the embryo, but removed in the model.

The thick stalk (dark grey) arising from the under surface of the tail end of the embryo is the **allantoic stalk, AL**: it attaches the embryo to the chorion and forms the embryonic part of the **placenta**, the organ by which the embryo obtains nourishment from the mother.

The swelling at the anterior end, between the head of the embryo and the yolk sac, is the **heart, H**: it consists of right and left halves, widely separate from each other. × 40.

**MODEL 2. Embryo lettered by Professor His, *L*, and estimated as about 14 days old.**

Greatest length of embryo 2·4 mm.

The **yolk sac**, the **amnion**, and the **heart** have been removed and the **allantoic stalk** cut short close to the embryo.

The form of the embryo is now well established ; the **head fold** and **tail fold** have increased considerably, and the **yolk stalk** (green), connecting the embryo with the **yolk sac**, is greatly reduced in diameter. The white rim bordering the embryo along its ventral edge represents the cut edge of the **amnion**.

The **neural canal** is closed along its whole length. The anterior end of the brain, or **fore-brain, BF**, is bent, through cranial flexure, nearly at right angles to the axis of the body, and forms the prominent rounded anterior end of the embryo.

At each side of the neck are two **visceral clefts**, represented as deep (red) grooves ; it is not certain whether they open into the pharynx. The anterior and larger of the two is the **hyo-mandibular cleft**, the posterior and smaller the **first branchial cleft**. The prominent transverse ridge in front of the hyo-mandibular cleft is the **mandibular arch, MN** : the shorter ridge between the mandibular arch and the fore-brain is the **maxillary arch, MX**. The strip of neck between the hyo-mandibular and first branchial clefts is the **hyoid arch, HY**.

The small pit above the dorsal end of the first branchial cleft is the commencing auditory vesicle, **AV**. The **stomodæal** or **mouth invagination, ST**, is the depression on the under surface of the head, immediately behind the fore-brain. It is bounded in front by the under surface of the head ; at the sides by the maxillary arches, which form the rudiments of the upper jaw ; and behind by the mandibular arches, which form the lower jaw, and meet each other in the mid ventral line at the place where the chin will subsequently be formed.

The **pericardial cavity, PC** (pink), lies on the ventral surface of the neck region, immediately behind the stomodæum and ventral to the gill clefts. The greater part of the wall of the pericardial cavity, and a part of the **heart** have been removed in the model.

Behind the pericardial cavity, and opposite the middle of the length of the embryo is the **yolk stalk** (yellowish green), which connects the embryo with the yolk sac. This has been, in the model, cut short close to the embryo so as to expose the **mid-gut, GM**, which is seen as a deep longitudinal groove on the ventral surface of the embryo.

The **allantoic stalk**, **AL**, which connects the embryo with the placenta, has been cut short, its proximal end alone being left as a short process (grey) on the ventral surface of the tail.

The **allantoic veins** (blue) are seen in section in the cut end of the allantoic stalk, and also running forwards along the sides of the body towards the heart. Just before reaching the heart they are joined by the **vitelline veins** (blue) from the yolk sac. × 40

**MODEL 3.** Embryo lettered by Professor His, **BB**, and estimated at about 16 days old.

Greatest length of embryo 3.2 mm.

The **amnion** and **yolk sac** have been removed ; the **pericardial cavity** opened from the ventral surface to expose the **heart** ; and the **allantoic stalk** cut across just before it reaches the **placenta**.

The most marked feature in the general form of the embryo is the sharp bend in the middle of the back, opposite the yolk stalk. A similar and equally marked bend has been noticed in other embryos of about the same age, but it is not yet certain whether it is to be regarded as a natural feature.

**Cranial flexure** is more marked than before ; the whole dorsal surface of the head being strongly convex, and the **fore-brain**, **BF**, carried round to the under surface of the head. The lateral swellings at the sides of the fore-brain are due to the **optic vesicles**, **OV**.

Three pairs of **gill clefts** are present, the **hyo-mandibular**, **first branchial**, and **second branchial** respectively.

The **stomodæal**, or **mouth invagination**, is now a wide transverse slit on the under surface of the head : it is bounded, as before, by the under surface of the head in front ; by the **maxillary arches**, **MX**, at the sides ; and by the **mandibular arches**, **MN**, behind.

The **heart** (red), which is of large size, lies on the under surface of the neck, and is exposed by removal of the ventral wall of the pericardial cavity : it is a single tube, twisted so as to form a loop, with the convexity towards the right side of the embryo. The posterior or horizontal limb of the loop is the **ventricular portion**, **V**, of the heart, and the anterior or oblique limb the **truncus arteriosus**, **TA**.



The **mid-gut** (green), **GM**, lies immediately behind the pericardial cavity, and is exposed by removal of the **yolk sac**, into which it opens. It is seen in the model as a deep longitudinal groove, continued forwards into the **fore-gut**, and backwards into the **hind-gut**. In its side walls are seen the cut ends of the **vitelline veins** (blue).

The **allantoic stalk**, **AL**, is seen as a great process depending from the under surface of the tail end of the embryo. It is cut across distally just before it reaches the placenta. In the cut end are seen the two **allantoic arteries** (red), which carry blood from the embryo to the placenta; the **allantoic vein** (blue), returning blood from the placenta to the heart; and the **tube of hypoblast cells** (yellow), which runs along the axis of the stalk. × 40

**MODEL 4.** Embryo lettered by Professor His, **M**, and estimated as about eighteen days old.

Greatest length of embryo 2·6 mm.

The **amnion** has been removed, but the **yolk sac** (yellow), **Y**, is present as a thin walled bag attached by a narrow stalk to the ventral surface of the embryo.

The **allantoic stalk**, **AL** (grey), is cut short close to the embryo: the ventral wall of the **pericardial cavity** has been removed to expose the **heart**, **H**.

The dorsal surface of the embryo is convex along its entire length, and shows no trace of the sharp bend in the middle of the back present in **Model 3**: the tail is also of rather greater length and prominence than in **Model 3**. In other respects the two embryos are closely similar, and the description already given of **Model 3** will apply to **Model 4** as well.

At the cut end of the **allantoic stalk** are shown the two **allantoic arteries** (red); the **allantoic vein** (blue); and the **core of hypoblast cells** (yellow) lining the allantois, and here constricted so as to form a solid rod. × 40

**MODEL 5.** Embryo lettered by Professor His, **Lr**, and estimated at about twenty days old.

Greatest length of embryo 4·2 mm.

The **amnion** and the **yolk sac** have been removed: the **allantoic stalk** cut across a short distance beyond the embryo; and the ventral wall of the **pericardial cavity** removed to expose the **heart**.

The embryo is considerably larger than those shown in Models **3** and **4**, but has not advanced much in development.

In the **head** the boundaries of the **brain vesicles** can be recognised fairly accurately. The **mid-brain, MB**, forms the rounded swelling at the top of the model; in front of it is the **fore-brain, BF**, the prominent swellings at the sides of which are caused by the **optic vesicles, OV**. Behind the mid-brain is the **hind-brain**, which is of considerable length, extending to the level of the first pair of **protovertebræ**.

The **olfactory pits, OL**, are a pair of shallow depressions at the sides at the extreme anterior end of the head, above the mouth. The **auditory vesicles, AV**, are represented as a pair of small rounded tubercles on the sides of the mid-brain, about the middle of its length, and opposite the second of the three gill clefts.

The same **three gill clefts** are present as in Models **3** and **4**, *i.e.*, the **hyo-mandibular, first branchial**, and **second branchial clefts**. In front of the hyo-mandibular cleft is the **mandibular arch, MN**, which extends down to the ventral surface of the head to meet its fellow of the opposite side at the chin. In front of the mandibular arch, and between it and the fore part of the head, is the **maxillary arch, MX**. The **stomodæal**, or **mouth invagination**, is a deep pit on the under surface of the head, somewhat squarish in outline; it is bounded in front by the fronto-nasal process, at the sides by the maxillary arches, and behind by the mandibular arches.

The **heart H** (red), is a single tube, very similar to that of model **3** but of larger size and more markedly twisted on itself.

The **mid-gut, GM** (green), lies immediately behind the pericardial cavity, and is exposed by removal of the yolk sac into which it opens. It is seen in the model as a tubular stalk into which open the **fore-gut** and **hind-gut**, in front and behind respectively. In the side wall of the mid-gut are seen the two **vitelline veins** (blue) cut across.

Opposite the yolk stalk the dorsal surface of the embryo is slightly concave, the concavity apparently corresponding to the sharp bend in the back seen in model 3.

At the cut end of the **allantoic stalk, AL**, are seen the two **allantoic arteries** (red), the **allantoic vein** (blue), and the solid rod formed by the **allantoic hypoblast** (yellow). Within, the allantoic vein divides into two veins (blue), which are seen in the model running forward in the body wall towards the heart.

The pair of longitudinal ridges running along the sides of the body ventral to the protovertebræ are the **Wolffian ridges**. Each of these is more prominent at two places, (1) opposite the posterior end of the heart and the anterior part of the mid-gut: (2) opposite the allantoic stalk. These more prominent parts of the Wolffian ridges are the rudiments of the **fore-limbs, FL**, and **hind-limbs, HL**, respectively. × 40.

**MODEL 6.** Embryo lettered by Professor His, **a**, and estimated as about 23 days old.

Greatest length of embryo, 4 mm.

The **amnion** has been removed, and the **yolk stalk** and **allantoic stalk** cut short close to the embryo.

The wall of the **pericardial cavity** has been removed so as to expose the heart.

The embryo is very completely rolled up on itself: the head and tail almost touch each other, and the outline of the entire embryo is approximately circular.

The head is very similar to models 4 and 5. The **mid-brain, MB**, forms the prominent knee-like angle at the end of the embryo. The **optic vesicles** lie close to the surface of the head, but the **lens** has not yet commenced to form. The **olfactory pits** are shallow depressions on the under surface of the fore part of the head, opposite to the heart. The **visceral clefts** and **arches** are the same as in models 4 and 5. The small rounded swellings above the hyoid arches are the **auditory vesicles, AV**.

In the body, the **protovertebræ** are indicated as squarish masses along the sides of the back: thirty-five pairs are shown, the full number

present at any period of development. Ventral to the protovertebræ are the **Wolffian ridges**, which, opposite the heart, and opposite the allantoic stalk, enlarge to form flattened outgrowths, the rudiments of the **arms**, **FL**, and **legs**, **HL**. The **heart** (red), which is exposed by removal of the wall of the pericardial cavity, is of large size: and the dorsal, or **auricular portion**, **A**, is marked off by grooves from the more ventrally placed **ventricular portion**, **V**.

On the left side of the model, below the tip of the tail, are seen the cut ends of the **yolk stalk** (yellow) which connects the embryo with the **yolk sac**, and the **allantoic stalk** (grey) which connects it with the placenta. In the cut end of the allantoic stalk are seen the **allantoic arteries** (red), the **allantoic vein** (blue), and the solid rod formed by the **allantoic hypoblast**. x 20

**MODEL 7.** Embryo lettered by Professor His, **R**, and estimated as **24** or **25** days old.

Greatest length of embryo, 5 mm.

The **amnion** has been removed, and the **yolk stalk** and **allantoic stalk** cut short close to the embryo. The **heart** has been exposed by removal of the wall of the pericardial cavity.

The back of the embryo has begun to straighten out, so that the head and tail are a good deal further apart than in model 6.

In the **head** the outlines of the **brain vesicles** are rather more distinct than before. The thin roof of the **hind-brain** is clearly indicated on the top of the head: the **mid brain**, **MB**, forms the prominent rounded swelling at the angle of the head, and the **fore-brain**, **BF**, with the **vesicles of the hemispheres**, forms the downwardly directed anterior end of the head.

The **hyomandibular**, **first branchial**, and **second branchial clefts** are very conspicuous in the side of the neck, and there is a slight indication of a **third branchial cleft** behind the **second branchial arch**.

The **mandibular arches**, **MN**, are long, and meet each other at the chin: the **maxillary arches**, **MX**, are small buds wedged in between the mandibular arches and the under surface of the head.

The **olfactory pits** are a pair of shallow depressions, with slightly thickened lips, at the sides of the fore part of the head. The

**auditory vesicles** are seen as a pair of small rounded swellings above the dorsal ends of the hyoid arches.

There are thirty-five pairs of **protovertebræ** present, as in Model 6. The **limb rudiments**, **FL**, **HL**, have increased considerably in size, and form two pairs of flattened buds, opposite the heart and the root of the tail respectively: the part of the **Wolffian ridge** connecting the two limbs of each side is less conspicuous than before. The **heart** (red) is much as in Model 6, but is of larger size: the division between the dorsal or **auricular**, **A**, and ventral or **ventricular portions**, **V**, is well marked. From the right hand end of the horizontal ventricular portion the **truncus arteriosus**, **TA**, runs forward to the under surface of the neck, where it divides into the several pairs of aortic arches, which are not shown in the model. On the right side of the embryo the cut ends of the **yolk stalk** (yellow), and the **allantoic stalk**, **AL** (grey), are shown, as in Model 7. × 20

**MODEL 8.** Embryo lettered by Professor His. **A**, and estimated at about twenty-seven days old.

Greatest length of embryo, 7·5 mm.

The **amnion** has been removed, and the **yolk stalk** and **allantoic stalk** cut short, close to the body of the embryo.

The stage illustrated by this model is an extremely characteristic one, all the more important organs being now established. The embryo, which is now four weeks old, is almost exactly the same size and at the same stage of development as a chick embryo at the end of the fourth day of incubation. The chief differences are the smaller size of the brain and of the sense organs, and especially of the eye in the human embryo. A rabbit embryo reaches the same stage of development, and the same actual size, on the twelfth day.

The embryo is rather more strongly flexed than in Model 7, the head and tail almost touching each other: this is largely due to the very sharp bend at the junction of the head and body.

In the head the **hind-brain** is of great length, extending forwards from the sharp bend just mentioned to the mid-brain: its anterior end, opposite the level of the maxillary arches, is the widest part of the brain, and gives origin to the **cerebellum**.



The **mid-brain, MB**, forms the prominent rounded swelling at the end of the head: below it is the **fore-brain, BF**, the anterior part of which is very wide owing to the rapidly growing **cerebral hemispheres, CH**.

The **olfactory pits, OL**, on the ventral surface of the hemispheres, are larger and deeper than before: each is bordered by a prominent tip, with a somewhat irregular outline. The small circular pit, with a thickened lip, between the olfactory pit and the maxillary arch, is the **lens, L**, of the eye. It is of much smaller size than in a chick embryo at the same stage.

The **auditory vesicles, AV**, are seen as a pair of small rounded protuberances on the sides of the head, just above the dorsal ends of the hyomandibular clefts.

The **visceral clefts and arches** are much as in Models **6** and **7**. The **maxillary arch, MX**, on each side is small and lies immediately behind the eye. The next, or **mandibular arch, MN**, is the largest of the series, and is partially divided by a constriction about the middle of its length. The **hyoid arch, HY**, is nearly as large as the mandibular, and is also constricted across its middle. The **first branchial arch BR 1**, lies behind the hyoid arch, and is of much smaller size. A still smaller **second branchial arch** is present, but is not shown in the model, being overlapped and concealed by the first. Of the visceral clefts the **hyomandibular cleft** is closed at this stage: the **first and second branchial clefts** are said to be open.

In the body the thirty-five pairs of **protovertebræ**, or **myotomes**, are shown. The tail is still free, and projects as a short conical process.

The **limbs, FL** and **HL**, are flattened buds, and show as yet no trace of a division into segments, or into fingers and toes. The outer surface of each limb is its extensor surface; and the inner surface, directed towards the body of the embryo, is the flexor surface. The root of attachment of each limb is seen to extend over four or five protovertebræ.

The **Wolffian ridge** connecting the arm and leg of each side is still present, but is inconspicuous.

The **heart** is seen through the thin wall of the pericardial cavity: the large swellings opposite the fore-limbs are the **auricles, A**, while the **ventricular portion** and the **truncus arteriosus** are more ventrally placed.

The swelling of the body behind the heart and fore-limbs is caused by the **liver, LI**, which is now of large size.

On the right side of the embryo, at the root of the tail, the cut ends of the **yolk stalk** (yellow) and the **allantoic stalk, AL** (grey), are shown: in the latter the **allantoic arteries** are coloured red, the **allantoic vein** blue, and the solid rod of **allantoic hypoblast** yellow.

× 20.

Description of a Series of Wax Models  
illustrating the Development of a

STARFISH  
(*Asterina gibbosa*.)

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CASE LXXXIV.

*The models are by Dr. Ziegler, from the drawings and descriptions of Professor Hubert Ludwig.\**

*The models are in each case 250 times the linear dimensions of the natural objects.*

*Asterina*, which is a common British starfish, lays eggs of an orange colour, and about 0.5 mm. in diameter. They are attached by glutinous egg membranes to stones, plants, etc., over which the female crawls, and are fertilised by the male as soon as they are laid. The female *Asterina* leaves her eggs to themselves, but many other starfish watch over theirs and guard them jealously until the young are hatched.

The actual rate of development varies with the temperature of the water. As a rule the *Asterina* larva hatches on the fourth day, leads a free swimming pelagic life for about a week, occasionally attaching itself, or crawling by means of the larval organ, and then, dropping to the sea-bottom, adopts the sluggish life of the adult.

The models illustrate the development during the pelagic period. Models 1 and 2 show the condition of the larva at the time of hatching

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\* Ludwig, "Entwicklungsgeschichte der *Asterina gibbosa*," *Zeitschr. Wiss. Zool.*, vol. 37, 1882; E. W. MacBride, "The Development of *Asterina gibbosa*," *Quart. Journ. Micr. Sci.*, vol. 38, 1896.

on the fourth day from the laying of the eggs : and models **10** and **11** illustrate the stage, on the tenth day, when the shape and structure of the starfish are becoming definitely established.

As in most Echinoderms there is a well-marked metamorphosis. The pelagic larva, as shown in models **5** and **6**, is bilaterally symmetrical, and shows no trace of the radiate symmetry so characteristic of the adult starfish. During the pelagic existence the starfish is gradually developed within the larva : many organs, including the mouth and anus, are formed anew, the larval ones disappearing : and finally, at the close of the pelagic life, large parts of the larva are absorbed much as the tail of the tadpole is absorbed during its conversion to a frog, and the form and habits of the adult starfish are acquired.

The colours of the models have in all cases the same significance :—

**Yellowish Brown** :—The external **epiblast**, whether of the larva or starfish.

**White** :—The **archenteron**, or primitive alimentary canal : white is also used in Models **6** to **11** for the calcareous spicules in the skin.

**Red** :—The **enterocœl**, or body cavity.

**Blue** :—The **hydrocœl**, or ambulacral system.

#### MODEL 1. Larva of the fourth day. just hatched.

The anterior end of the larva, directed upwards in the model, is slightly cupped : and is bordered by a thickened rim, the commencement of the **larval organ**, **LO**, of the later stages. This rim is somewhat obliquely placed, being highest on the dorsal surface of the larva, lowest on its ventral surface : the rim is covered by very long cilia, not shown in the model, and is the swimming organ of the larva.

On the ventral surface, just behind the ciliated rim, is a pocket-like depression, **ST** : this is the **stomodæum**, or mouth invagination : it does not yet open into the digestive canal.

#### MODEL 2. The dorsal half of a larva of the same age as Model 1.

The outer wall of the embryo (crown), is formed by the **epiblast**. The cavity with white walls in the posterior part of the embryo is the

**archenteron**, **GA**, or **gastrula cavity**, the primitive digestive cavity: it opens to the exterior at the hinder end of the embryo through the **blastopore**, **BL**, an exceedingly narrow passage. From the anterior end of the archenteron a large thin-walled diverticulum (red) arises: this is the **enterocœl**, or body cavity, **EC**: it extends forwards to the anterior end of the embryo, and backwards as two lateral pouches along the right and left side of the archenteron. Its walls form the **mesoblast**, or middle germinal layer of the embryo.

The body cavity, or **cœlom**, of an animal is called an **enterocœl** when it arises, as in *Asterina*, as an outgrowth or outgrowths from the alimentary canal or **enteron**. A body cavity which arises, as in the chick, through splitting of an originally continuous sheet of mesoblast into two layers, is called, in contradistinction, a **schizocœl**.

### MODEL 3. Larva of the fifth day.

The epiblast of the left side of the body has been removed, to expose the alimentary canal and the walls of the body cavity.

The larva has increased in length, mainly through growth of the **larval organ**, which now forms a prominent thickened rim at the anterior end of the larva: it is placed much more obliquely than at the earlier stage, its dorsal edge projecting forwards far in front of the ventral edge.

The **enterocœl**, **EC**, has grown considerably. It consists of (1) a median anterior part, which still opens into the anterior end of the archenteron, **GA**, and which extends forwards into the larval organ: and (2) a pair of lateral pouches, which lie along the sides of the archenteron, and extend to the hinder end of the embryo.

The **archenteron** (white), **GA**, lies in the middle of the larva, between the right and left enterocœl pouches. At its hinder end the **blastopore** has closed, and the archenteron is completely separated from the surface. The archenteron, therefore, at this stage has no communication with the exterior, though it still opens freely into the body cavity or enterocœl.

The **stomodæum**, or mouth invagination, **ST**, is seen in section as a deep, but narrow, pocket-like depression of the epiblast on the



ventral surface of the larva, just behind the thickened rim of the larval organ. The bottom of the pit lies very close to the archenteron, but does not yet open into this.

Model 4 has been omitted from the series. It represented a surface view of the same larva as that shown in Model 5.

#### MODEL 5. Larva of the sixth day.

The body wall of the left side has been in great part removed, to expose the internal organs.

The change in shape of the embryo as compared with Model 3, and especially the increase in length, are due almost entirely to further growth of the **larval organ, LO**, which forms a conspicuous thickened rim, projecting far forwards at its dorsal border. The anterior end of the larva, surrounded by the rim, is depressed; but rises up as an ovoid swelling opposite the body of the larva. The larval organ and the whole anterior end of the body are very flexible in the living embryo, bending freely in all directions.

[The disc for fixation is an organ which appears in the centre of the larval organ at this stage. (See MACBRIDE, *Op. cit.*, p. 347)].

The larva swims freely by means of the long cilia on the larval organ, and occasionally crawls along the sea bottom, using the larval organ as a sucker.

The **archenteron, GA** (white), is a sac lying in the middle of the larva. It ends blindly behind, but now opens to the exterior at the **mouth ST**; the stomodæal pit of the earlier stage, Model 3, having met the archenteron and opened into it. The **mouth opening, ST**, is a small round aperture on the mid-ventral surface, just behind the thickened rim of the larval organ.

The **enterocœl** (red) has separated completely from the archenteron. In front, it forms, as before, a single cavity, which extends forward into the larval organ: posteriorly the two lateral pouches of Model 3 have grown so as to completely surround the archenteron: they meet and open into each other on the ventral surface of the larva; on the dorsal surface the two cavities remain distinct, but their walls meet and fuse to form an obliquely placed septum or mesentery, slinging the archenteron to the dorsal body wall. The left enterocœl is from

the first larger than the right, and, growing more rapidly than the latter, occupies the posterior end and dorsal surface of the larva. The right enterocoel is smaller, and lies on the right side and ventral surface of the larva.

In the model, the left body wall has been removed so as to show the enterocoelic pouches. The cavity, **EC**, at the posterior end of the larva is part of the left enterocoel, and is seen to be separated in front from the right enterocoel by an obliquely placed **septum**.

The **hydrocœl**, **HC**, (blue), is a flattened pouch-like outgrowth from the left enterocoel, lying on the left side of the body, immediately beneath the surface epiblast. The hydrocœl is the first commencement of the **ambulacral system** of the starfish. It is notched at its margin into five lobes, which by further elongation become, in later stages, the five radial ambulacral vessels.

[MacBride has discovered that there is also a small right hydrocœl which persists in the adult as a closed sac under the madreporite.]

The **dorsal pore**, **DP**, is a small circular hole in the body wall, on the dorsal surface of the larva, a little to the left of the median plane, and almost exactly opposite the mouth. It leads from the exterior into the left enterocoel.

The most important points shown in Model 5 are, (1) the origin of the ambulacral system as a specialised portion of the body cavity: (2) the fact that the dorsal pore, which corresponds in position to the madreporic plate of the starfish, does not at first open directly into the ambulacral system, but only indirectly through the body cavity.

#### MODEL 6. Larva of the eighth day.

The whole larva has grown considerably. The **larval organ** is of great size, but has already commenced to degenerate, its surface being thrown into irregular folds.

The body of the larva is separated by a slight constriction from the larval organ, and is already showing indications of the stellate form of the adult starfish. On the left side there is a large and well-defined five-lobed swelling formed by the left **hydrocœl**, the structure of which is shown in Model 7. The **larval mouth** has closed up, and as the adult mouth is not yet formed, the alimentary canal has at this

stage no communication with the exterior. The **dorsal pore** is seen as a minute opening on the dorsal edge of the larva, just below the larval organ.

On the right side of the body of the larva the stellate form of the adult starfish is already apparent. The small white branched patches represent the commencing **calcareous plates** of the future aboral surface. Of these plates there are eleven present at this stage: one placed somewhat below the middle is the **dorso-central plate, DC**. Five others, placed radially, in the blunt processes which mark the commencing arms of the starfish, become the **terminal plates, TP**, of the tips of the arms, moving out along these as they lengthen. The remaining five plates are smaller, interradian in position, and known as the **basals, BP**: one of these, **AM**, which lies at present a short distance to the right of the dorsal pore, will at a later stage grow round this and form the **madreporic plate** of the adult.

#### MODEL 7. Larva of the eighth day.

For a description of the external characters see model 6. The integument of the left side has been removed so as to expose the ambulacral system (blue), the body cavity (red), and the alimentary canal (white).

The alimentary canal (white), **GA**, is a closed sac, lying in the middle of the body: it has no communication with the exterior, but from its left side near the anterior end, a diverticulum, the **œsophagus, OE**, arises, and grows towards the surface. This is seen in the model lying in a notch in the anterior border of the left hydrocoel, **HC**: it is at present blind, but will at a later stage open to the surface and form the adult **mouth**.

The **cœlom** (red) consists, of a large median anterior portion, the **anterior cœlom**, a small right and large left **hydrocœl** and a right and left posterior cœlomic sac or **enterocœl**. These latter now completely surround the alimentary canal, occupying the whole space between this and the body wall: the right and left sacs open freely into each other, but are still separated along the right side by a **septum**, or mesentery, which slings the alimentary canal to the body wall. This septum, which now runs antero-posteriorly, along the right side of the larva, can be seen at the lower end of the model: it corresponds to the oblique septum of Model 5.

The **left hydrocœl, HC**, is now constricted off from the enterocœl : it forms a flattened sac, somewhat horse-shoe shaped, with the œsophagus, **OE**, lying between its arms : it gives off from its outer border five diverticula, of which the posterior one, lowest in the model, is the largest, and is slightly lobed at its sides to form the rudiments of the **tube feet**.

The **dorsal pore, DP**, now communicates with the hydrocœl by a definite **madreporic tube**, down which a bristle has been passed in the model.

The **madreporic tube** is formed first as a groove along the inner wall of the hydrocœl : by fusion of its lips the groove becomes a tube, which opens at one end into the hydrocœl, and at the other into the enterocœl, close to the opening of the dorsal pore. These two latter openings soon become continuous, by boxing in of the part of the enterocœl between them, and in this way the complete madreporic tube is formed.

#### MODEL 8. Larva of the tenth day.

The metamorphosis is now in active progress. The **larval organ, BO**, is much shrunken, and greatly reduced in size. It ultimately becomes entirely absorbed, giving rise to no part of the adult. During its absorption there is no mouth or opening of any sort into the alimentary canal : and the young starfish lives on the larval organ, much as the young frog is nourished for a time by absorption of its tail.

The **body** of the larva is now rapidly assuming the shape of the starfish, and the relations of larva and adult to each other should be carefully noticed. Comparison of Models 6 and 8 shows that the **aboral or ant-ambulacral surface of the starfish**, is formed from the **right side of the larva** ; while the **oral or ambulacral surface of the starfish**, indicated in the early stages by the left hydrocœl, is formed from the **left side of the larva**.

As shown in the model, the oral and aboral surfaces of the starfish are at first not exactly parallel or opposite to each other, but placed somewhat obliquely.

On the **oral, or ambulacral surface**, the left hydrocœl has greatly increased in size, and now occupies almost the whole surface :

the rounded swellings at its margin are the commencing **tube feet**, arranged in five groups corresponding to the five radial diverticular of the hydrocœl seen already in Model 7. The white patches lying in pairs between the tube feet are the commencing **ambulacral ossicles**.

On the **aboral**, or **ant-ambulacral surface**, the **dorso-central plate**, **DC**, the five **terminal plates**, **TP**, and the five **basal plates**, **BP**, are seen as described in model 6. The **dorsal pore**, **DP**, which was previously on the dorsal edge of the larva (compare Models 5 and 6) has shifted on to the ant-ambulacral surface: the basal plate, **BP**, lying immediately to its right ultimately grows round the dorsal pore and becomes the **madreporic plate**.

#### MODEL 9. Larva of the tenth day.

For a description of the external characters see model 8. The aboral surface of the starfish, formed from the right side of the larva, has been removed to expose the alimentary canal, the body cavity, and the madreporic tube.

The **alimentary canal**, **GA**, lies in the middle of the starfish. It is a closed thin-walled sac, produced at its margin into five radial pouch-like diverticula. It is attached to the body wall by a septum, or **mesentery**, which runs obliquely across its aboral surface, and which marks the line of meeting of the walls of the right and left halves of the body cavity, or enterocœl (compare Models 5 and 7).

At the upper, or anterior end of this mesentery is the **madreporic tube**, **MT**, into which a bristle has been inserted: it leads from the **dorsal pore** on the aboral surface to the **hydrocœl** on the oral surface.

#### MODEL 10. Larva at the end of the tenth day.

The metamorphosis is now practically completed. The **larval organ**, **LO**, is almost entirely absorbed, and is present as a mere stump attached interradially to the oral surface of the starfish.

The **oral surface** is smooth and imperforate: the mouth being not yet formed. Round the margin are the five groups of **tube feet**, which have increased considerably in size. Each group consists at this stage of a single median lobe, which becomes the **terminal tentacle** at the tip of the arm of the adult, and two pairs of rounded



**tube feet.** As the arm grows, other pairs of tube feet will be formed in succession between those already present and the central disc of the starfish. The white stellate patches at the bases of the tube feet are the commencing pairs of **ambulacral ossicles**.

The **aboral surface** is smooth, well defined, and markedly pentagonal in outline, the angles marking the radii and corresponding to the groups of tube feet on the oral surface. In the left interradius is the opening of the **dorsal pore, DP**: the deep groove in front of it in the model is apparently an accidental exaggeration of the depressions seen in the other interradiar areas. The calcareous plates are the same as in Models **6** and **8**; a **dorso-central plate, DC**, five **terminal plates, TP**, and five **basal plates, BP**, one of which, **AM**, will become the **madreporic plate** at a later stage.

#### MODEL 11. Larva at the end of the tenth day.

For a description of the external characters see Model **10**. The oral, or ambulacral wall, of the starfish has been removed to expose the ambulacral system, the œsophagus, and the body cavity.

The **œsophagus, OE**, lies in the centre of the oral surface: it is a thick walled diverticulum of the alimentary sac (compare Model **9**), which is in close contact with the body wall, but does not yet open to the exterior.

The left **hydrocœl, HC**, is horse-shoe shaped (compare Model **7**), and closely surrounds the œsophagus below and at the sides: from it five radial diverticula arise, which become the five **radial ambulacral vessels** of the adult, and which give rise laterally to the **tube feet**.

The small round hole, **MT**, in the roof of the left arm of the hydrocœl, is the opening of the **madreporic tube**, which arises from the **dorsal pore, DP**, on the aboral surface.

The **body cavity** is opened in front of the œsophagus, and is seen to be prolonged forwards into the stump of the larval organ.

About two days later than the stage shown in Models **10** and **11**, the **mouth** of the starfish is formed in the middle of the oral surface: the **anal opening** forms a few days later.

The **arms** rapidly increase in size, and as they grow the five radial diverticula of the alimentary sac, seen in Model **9**, extend into them:

each diverticulum divides into two branches, which acquire glandular walls, and become the arborescent **pyloric diverticula** occupying the arms of the adult.

The two arms of the horse-shoe shaped left hydrocoel (compare Models **7** and **11**) meet and unite about the twelfth day, so as to complete the annular **circumoral ambulacral vessel**. The ring encloses the stalk of the **larval organ**, which, therefore, lies on the oral surface, very close to the mouth, but which soon disappears completely.

The **tube feet** rapidly increase in number as the arms elongate. They have at first no **suckers**, and indeed do not acquire these until the fifth or sixth week. The terminal tentacles never develop suckers.

Description of a Series of Wax Models illustrating  
the Form and Structure of some of the  
more Important Types of

# MARINE PELAGIC LARVÆ.

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CASE LXXXIV.

*The Models are by Dr. Ziegler, from the figures and descriptions, and in part under the superintendence of Professors Metschnikoff,\* Selenka, Lang, Hatschek, and Johannes Müller.*

The great majority of marine invertebrates lay eggs of small size, which hatch as minute pelagic larvæ, swimming freely by means of cilia, clothing the whole or part of their surface. These pelagic larvæ usually differ very markedly in form, in structure, and in habits from the adult; and in many cases pass through a more or less abrupt metamorphosis before reaching the adult state.

Certain types of these larvæ are of very widespread occurrence, the Trochophore larva, for instance, being characteristic of Annelida and Mollusca, and occurring in Gephyrea, Polyzoa, and other groups as well: and this resemblance, amounting almost to identity, in the early stages of existence, often affords most important clues to the real relations of animals, which, when adult, appear to be constituted on entirely different plans.

These pelagic larvæ are characterised by their minute size, their glassy transparency, their ciliated external surface, and the absence of

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\* Metschnikoff, "Studien über die Entwicklung der Echinodermen und Nemertinen," *Mém. Acad. Sci. St. Pétersbourg*, vol. 14, no. 8, 1869.

jaws or other organs for the prehension and mastication of food. They occur in enormous numbers, and form the staple food-supply of a great variety of marine animals.

In all the models the larva is represented as bisected by a median sagittal plane, the right half of the larva being alone shown.

The colours of the models have in all cases the same signification :

**Blue :—Epiblast**, or organs of epiblastic origin.

**Red :—Hypoblast**, or organs of hypoblastic origin.

**Yellow :—Mesoblast**, or organs of mesoblastic origin.

Cilia when of special size, are represented by bristles : in other cases either by dots or by a deeper blue colour of the surface.

### MODEL 1. *Pilidium* Larva of a Nemertine Worm.

*The model is prepared from the figures of Professor Metschnikoff.*

The adult Nemertine, a species of *Cerebratulus*, is a slender elongated worm about two inches long, of a milk white colour, with reddish spots at the anterior end.

The *Pilidium* larva is shaped something like a cap or helmet, with anterior, **AL**, and posterior, **PL**, lobes, and a pair of large rounded lateral lobes, **LL**, depending from the sides. The whole surface of the larva is ciliated, the **cilia** being especially large round the margin of the larva and of its lobes, indicated in the model by the deeper blue colour. From the apex of the larva a long spike-like, but freely moveable **flagellum** projects upwards.

The **mouth** is a large aperture in the middle of the ventral surface : it leads into a ciliated **œsophagus**, **OE**, which, passing upwards and backwards, opens into a spherical **stomach**, **S**, lying in the posterior half of the larva, and having its walls formed of glandular epithelial cells. There is no intestine or anus.

Two pairs of pit-like invaginations of the skin are present on the ventral surface ; of which the two of the right side are seen in the model. One pair, the **prostomial invaginations**, **PI**, lie in front of the mouth ; the other pair, or **metastomial invaginations**, **MI**, are behind it.

The mouths of these invaginations soon close, so that they become closed sacs, which rapidly increase in size. The two prostomial sacs soon meet, and open into each other; the two metastomial sacs do the same; and finally the prostomial and metastomial sacs meet each other above the alimentary canal, and their walls coalesce. From the first the outer walls of the sacs, next the skin of the embryo, are thin; while the inner walls, next the alimentary canal, are much thicker. After coalescence of the sacs their outer walls form a thin continuous membrane, the **amnion**. The inner, thicker wall of the fused sacs grows round the alimentary canal, and becomes ultimately the skin of the adult Nemertine, which is thus formed within, or rather cut out of the middle of the larva: the internal organs of the larva being appropriated by the adult, but an entirely new external skin being formed.

The Nemertine continues developing within the larva for some time; increasing in length, and gradually acquiring its worm-like shape. Ultimately the Nemertine, which has now the shape and structure of the adult, frees itself from the larval skin, drops to the bottom of the sea, and adopts the mode of life of the adult.

The Pilidium larva is specially characteristic of the Nemertines, though not universal in the group. A form closely similar to it occurs in many of the marine Turbellarians. The two chief points about it are the central position of the mouth, and the absence of an anus: these have led to a comparison of a Pilidium with a jelly fish.

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## MODEL 2. The Pelagic larva of *Yungia aurantiaca*, often spoken of as Müller's larva.

*The model is prepared from the figures and under the direction of Professor Lang.\* It is about 200 times the linear dimensions of the natural object.*

*Yungia*, one of the largest of the Turbellaria, is a flattened oval worm, measuring about 5 cm. in length and 3 cm. in breadth. It is found crawling over stones at shallow depths in the Mediterranean.

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\* Lang, "Die Polychaeten des Goltes von Neapel," *Fauna und Flora des Goltes von Neapel*, 1884.



The **eggs** are small and numerous: they are laid during the summer months, in encrusting layers cemented to the sea weeds, stones, etc., over which the animal crawls. The young hatch in about twelve days as minute free-swimming pelagic larvæ, and very speedily reach the stage shown in the model.

The **larva**, which now measures 0·06 to 0·08 mm. in length, has a somewhat pyriform body, the broader end being anterior, and marked by a long spike-like **flagellum**. The body is produced at its equator into **anterior, AL**, and **posterior, PL**, lobes, as in *Pilidium* (Model 1): but in place of the single lateral lobe on each side, there are three flattened finger-like processes **L 1, L 2, L 3**.

The whole surface of the larva is ciliated, the cilia being of exceptional size round the margins of the lobes, and along a band which connects the bases of the lobes with one another, indicated in the model by the darker blue colour.

The **mouth** is a small aperture on the ventral surface, just behind the overhanging anterior lobe **AL**: it leads into a straight ciliated **stomodæum, ST**, opening at its inner end into the **stomach, S**. This latter, red in the model, is a sac with thick glandular and ciliated walls; it is lobed along its sides, and gives off a well-marked anterior diverticulum, extending to the anterior end of the body; and a less prominent posterior diverticulum.

Surrounding the stomodæum, like a collar, is the **pharynx, P**, a very characteristic Turbellarian structure, formed as an annular fold, at the junction of the stomodæum and stomach.

The space between the external epiblast and the hypoblastic wall of the alimentary tract is filled up by a solid mass of **mesoblast, M** (yellow), consisting chiefly of muscle fibres and branching connective tissue cells. This great development of the mesoblast is one of the chief differences between the Turbellarian larva and the other larvæ of the series.

In the anterior part of the body is a large **nerve ganglion**, or "brain," **B**, from the upper end of which a large **sensory nerve** is represented running towards the skin. A number of **eyes** are present represented by black spots in the model, and arranged in small groups at the anterior pole of the larva.

The further development of the Turbellarian larva is a gradual one, there being no abrupt metamorphosis. The larva elongates considerably; the ciliated lobes become less prominent, and the body flattened. A sucker is formed on the ventral surface behind the mouth, and by this the larva attaches itself temporarily, though very firmly, to rocks or other solid bodies. Gradually the worm adopts a crawling rather than a swimming mode of locomotion: the ciliated lobes are absorbed, and the adult form and habits established.

Larvæ similar to the above occur in other genera of marine Turbellaria, and appear to be characteristic of the group.

### MODELS 3 and 4. Trochophore larva of Polygordius.

*The models are from the figures and descriptions of Professor Hatschek.\**

*They are in each case about 150 times the linear dimensions of the natural objects.*

Polygordius belongs to the group of marine worms, for which Hatschek has proposed the name Archi-annelida; they differ from the ordinary segmented worms, or Annelida, in being devoid of the chitinous setæ so characteristic of annelids generally, and in having no external ringing or annulation of the body, although internally it is divided into segments by septa.

**MODEL 3. An early Trochophore larva of Polygordius, shortly after hatching.**

The **larva** is a flattened sphere with a small conical knob at its lower pole, really the posterior end of the animal. Round the equator are two parallel ciliated bands, of which the upper or **præoral band** is double, and the lower, or **postoral band**, single. The cilia of these bands are of large size, and are represented in the model by dots. Between the præoral and postoral bands is a zone, dark blue in the model, covered with fine cilia.

The **mouth** is a small aperture on the mid-ventral surface, in the ciliated zone just mentioned, and between the præoral and postoral bands: it leads into a short straight **œsophagus, OE**, opening into

\* Hatschek, "Studien über Entwicklungsgeschichte der Anneliden," *Arch. Zool. Anat. Microsc.* vol. 1, 1878.

a globular **stomach, S**, from which a short **intestine** leads to the anus, in the centre of the conical knob marking the hinder end of the body.

At the opposite or anterior pole is a thickened patch of epiblast, **N**, the commencing **nerve ganglion**, in connection with which a pair of eyes, and a branching system of nerve fibres, not represented in the model, are already present.

Between the external epiblast and the hypoblastic wall of the alimentary canal there is a wide space. In this space, at the hinder end of the larva, and at the sides of the intestine, lie the paired **bands of mesoblast, M** : these are at present solid plates of cells growing forwards from a pair of **primary mesoblast cells** wedged in between the epiblast and hypoblast, one on each side of the anus.

Immediately in front of each mesoblast band, and attached to its anterior end, is the **head kidney**, a ciliated tube opening to the exterior at its hinder end, and splitting in front into two branches, which open by funnel-shaped mouths into the body cavity, or rather into the space between the epiblast and the alimentary canal.

#### MODEL 4. Later Trochophore larva of *Polygordius*.

As compared with the earlier larva shown in Model 3, the chief differences are the following :—

The larva has increased in size, the two models being made to the same scale. The posterior end of the larva, a small conical process in Model 3, is now of considerable length, the alimentary canal becoming drawn out to keep pace with the growth of the body.

The **mesoblast bands, M**, have increased considerably in size. Each is triangular in shape, with the base upwards, and the apex formed by one of the primary mesoblast cells at the hinder end of the body. Each mesoblast band is divided transversely into **segments** ; of these the anterior and widest ones are the oldest, while new ones are intercalated at the posterior end, in front of the primary mesoblast cells, and budded off from these.

The **head kidney, K**, lies as before at the anterior end of the mesoblast band of each side. It has increased in size ; and each of its primary branches has subdivided, and now opens into the body cavity by three funnel-shaped mouths.

The **nerve ganglion, N**, at the anterior pole of the larva is of larger size than before, and **nerve fibres**, can be traced passing from it to various parts of the body.

The further development of *Polygordius* is effected by rapid elongation of the hinder end of the body, by which the vermiform shape of the adult is gradually acquired. At the same time the præoral ciliated band becomes less conspicuous: the anterior end of the body more pointed; and the mouth more nearly terminal in position: while a pair of cephalic tentacles grow out from the anterior end of the animal.

The number of mesoblastic segments becomes greatly increased; the segments themselves become hollow; the corresponding ones of the two sides meet and open into each other; and by further dilatation of their cavities the several compartments of the body cavity of the adult are formed, while the walls of adjacent segments fuse to form the septa.

The duct of the head kidney grows back along the whole length of the body as a tube, which is at first straight, but soon becomes sinuous, and then divides into a series of short lengths which correspond to the segments, and become the segmental or excretory organs of the adult.

The early Trochophore larva shown in Model 3 corresponds therefore to the two extremities, oral and anal, of the adult worm; the whole of the rest of the length of the worm, all the segmented part in fact, being intercalated between these two ends during the development of the larva.

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#### MODEL 5. Trochophore larva of *Eupomatus uncinatus*.

*The model is from the figures and descriptions of Professor Hatschek.\**

*Eupomatus* is one of the Serpulida, a group of marine tubicolous Annelids. The white twisted calcareous tubes of an allied genus, *Serpula*, are frequently seen attached to the outer surface of oyster shells.

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\* Hatschek, "Entwicklung der Trochophora von *Eupomatus uncinatus*," *Arch. Zool. Inst. Wien*, vol. 6, 1885.

The **eggs** are of small size, and develop very rapidly. At the end of the first twenty-four hours the young larva escapes from the egg membrane, and by the fourth day it has reached the stage shown in the model.

The **larva**, which agrees in most respects with that of *Polygordius*, Model 4, is pear-shaped, with a rather blunt anterior end, and a rather more pointed posterior end.

The distribution of the **cilia** on the surface is indicated by the darker blue colour. A tuft of very long cilia or flagella, indicated in the model by bristles, marks the anterior pole; and a similar though smaller tuft is present at the posterior pole. As in the *Polygordius* larva, a double **præoral ring** of large cilia runs round the equator or widest part of the larva, and is indicated by dots in the model. Midway between the præoral ring and the posterior end of the body is the second or **postoral ring** of large cilia, also indicated by dots, and much further back than in *Polygordius*. The whole of the belt between the præoral and postoral rings is covered with fine cilia, which extend back along the mid-ventral surface almost to the hinder end of the body.

In the middle of this belt, on the ventral surface, is the large **mouth** opening, towards which the cilia sweep the minute particles on which the larva depends for food. The mouth leads into a wide **œsophagus**, **OE**, opening into the **stomach**, **S**; from this the intestine, **I**, runs back to the hinder end of the body, opening at the **anus** on the dorsal surface, slightly in front of the hinder end of the body.

The **mesoblast** is only slightly developed; it consists of a pair of small masses of rounded cells (yellow) lying at the side of the hinder part of the intestine, and formed, as in *Polygordius*, by division of a pair of primary mesoblast cells, wedged in between the epiblast and hypoblast, at the sides of the anus.

The **head kidneys**, **HK**, are a pair of ciliated tubes, said to be formed by elongation of single mesoblast cells. The anterior end of the head kidney is in close relation with the œsophagus, and the posterior end with the mesoblast: it is uncertain whether the ends of the tube are open at this stage.



At the hinder end of the body is a closed sac, the **anal vesicle, AV**. This is formed at an early stage of development as a vacuole or cavity in the substance of the epiblast cells, and attains a considerable size. It has no connection with the alimentary canal, or with any other organ, and it disappears completely at a slightly later stage. It appears to be characteristic of the larvæ of Serpulida.

There is a prominent thickening of the epiblast to form a **nerve ganglion, N**, at the anterior pole of the larva: and a ring-like thickening, **NN**, opposite the præoral band of cilia, is regarded by Kleinenberg and others as probably a **præoral nerve ring**.

Two groups of **eyes**, represented in the model by black spots, are present on the sides of the anterior part of the larva.

A pair of **auditory vesicles, E**, are present as closed sacs, formed from the epiblast on the ventral surface of the larva, a little way behind the mouth. Stiff hairs project from the walls of the vesicles into their cavities, which are filled with fluid and certain small otoliths.

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### MODEL 6. Trochophore larva of Tereido.

*The model is from the figures and descriptions of Professor Hatschek,\* and is about 500 times the linear dimensions of the natural object.*

Tereido, commonly known as the 'ship-worm,' is a marine Siphonate Pelecypod, which dwells in long tubular burrows that it excavates in submerged timber. It occurs very abundantly, and does immense harm to wooden piers, and to ship timbers, boring through them in all directions.

The adult animal has a small body, half an inch or so in length, enclosed in a bivalved shell: the siphons or respiratory tubes, formed by elongation of the hinder end of the animal, are enormously developed, being a foot or more long.

The young leave the eggs as free swimming pelagic larvæ, with the form and structure shown in the model. While still of very small size, they attach themselves to timber, and begin boring their way into this. As the young Tereido increases in size it bores deeper and

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\* Hatschek, "Ueber Entwicklungsgeschichte von Tereido," *Arb. Zool. Inst. Wien*, vol. 3, 1880.

deeper, and makes a wider hole. It bores into the timber for the sake of obtaining a suitable habitation, and it depends for food, like other Pelecypods, on minute particles swept in along the siphons by ciliary action.

In general structure the **larva** closely resembles the Trochophore larvæ of Polygordius or of Eupomatus, Models 4 and 5.

The anterior end is broad and flat, the posterior end conical. The **cilia**, which in the earlier stages covered the whole surface, are now restricted to an equatorial band, bordered in front by a double **præoral ring**, and behind by a single **postoral ring** of specially long cilia, indicated in the model by dots. A small ciliated patch is present on the ventral surface in the region of the anus; and a tuft of specially large cilia or **flagella**, represented by bristles in the model, arises from the centre of the anterior end of the larva.

The **mouth** is a large opening on the ventral surface in the ciliated belt between the præoral and postoral rings: it leads into a straight **œsophagus**, **OE**, opening into a large globular **stomach**, **S**, from which the **intestine**, **I**, runs to open at the **anus**, on the ventral surface a little distance in front of the hinder end.

The **mesoblast**, **M**, consists, as in Polygordius and Eupomatus, Models 4 and 5, of two small masses of rounded cells lying at the sides of the intestine, and of which the mass of the right side is alone shown in the model. The mesoblast masses arise, as in Annelida, from a pair of **primary mesoblast cells** at the sides of the anus. In other parts of the larva, especially near its anterior end, branched cells occur in the space between the epiblast and the alimentary canal. These cells, which are not represented in the model, and the mode of origin of which is not very clearly made out, take part in the formation of mesoblastic structures.

The **head kidneys**, **K**, are a pair of short ciliated tubes, of which the one of the right side is alone shown in the model. Each kidney is formed from one or more of the mesoblast cells; it opens at its hinder end to the exterior, and at its anterior end into the coelom by a funnel shaped mouth, not yet made out very definitely.

In the middle of the anterior end of the larva, opposite the big tuft of cilia is the bilobed **nerve ganglion**, **N**, formed by thickening of

the epiblast, and apparently corresponding to the cerebral ganglia of the adult. From the ganglion, at a slightly later stage, nerve fibres radiate outwards to various parts of the body. Opposite the præoral ring of cilia, the epiblast is markedly thickened, but whether this thickening is nervous, as in *Eupomatus*, is uncertain.

The **shell, SH**, is present as a thin cuticular cap covering the dorsal surface of the larva. In the early stages of development, the shell is a median structure; but, about the period represented by the model, it becomes folded along the middle line into right and left halves, the line of the folding corresponding to the hinge of the adult shell.

Trochophore larvæ, essentially similar to that shown in Model 6, occur widely amongst marine Mollusca. They are very characteristic of both Pelecypods and Gastropods, but do not occur among the Cephalopods, in which the early stages are much modified through the presence of food yolk. The resemblance between the Trochophore larva of a Mollusc (Model 6) and that of an Annelid (Model 4), is very striking. The only important point of difference is the presence of the shell in the former, to which the slightly altered position of the anus is almost certainly due. The agreement is far too close to be accidental, and is probably rightly interpreted as indicating a genetic relationship between these two great groups of Invertebrates.

## MODEL 7. Trochophore larva of *Pedicellina echinata*.

*The model is from the description and figures of Professor Hatschek:\**  
*the following description is, however, based largely on the more*  
*recent account given by Dr. Harmer. The model is about*  
*350 times the linear dimensions of the actual object.*

*Pedicellina* is a small marine Polyzoan. It is colonial in habit, consisting of a stolon of branching tubes attached to sea weeds, shells, zoophytes, etc., from which arise short erect stalks, bearing the polypides at their apices; polypide and stalk together measuring about 1 mm. in length.

\* Hatschek, "Embryonalentwicklung und Knospung des *Pedicellina echinata*," *Zeitschr. wiss. Zool.*, vol. 29, 1877; Harmer, "On the Life-history of *Pedicellina*," *Quart. Journ. Micr. Sci.*, vol. 27, 1886.

Pedicellina is one of the few members of the Entoprocta, a group of Polyzoa in which both mouth and anus lie within the ring of tentacles, and the tentacles, when the animal is disturbed, are not retracted but merely rolled up.

The **larva** is roughly spherical in shape. The anterior end is rounded: it bears in its centre a conical projection, **CO**, with a slightly cupped apex, surrounded by a circle of strong cilia, represented in the model by bristles. This structure spoken of by Hatschek as a 'sucker,' and by Balfour as the 'ciliated disc,' is apparently a **sense organ**, and is perhaps, equivalent to the apical sense organs of Models **1** to **6**.

The body is encircled, a little below its equator, by a thickened ring, **PR**, well seen on the outer surface of the model, and bearing a circle of specially large cilia. It appears to correspond to the **præoral ring** of other Trochophore larvæ.

The whole of the body behind the præoral ring is ciliated; indicated in the model by the darker blue colour. In the retracted condition of the larva, the whole of this part can be drawn back, forming a cup-like depression, the **vestibule**, the margin of which is formed by the thick ciliated præoral rim.

The **mouth** is in the mid-ventral line, just behind the præoral ring: it leads into a short **œsophagus**, **OE**, which runs upwards to the globular **stomach**, **S**. The **rectum**, **R**, is a straight tube running back from the stomach to the **anus**, placed at the apex of an **anal cone**, **AC**, which forms a prominent projection on the surface of the body.

The œsophagus and rectum are formed by invaginations of the skin, called **stomodæum** and **proctodæum** respectively, and are hence lined by epiblast. The stomach is formed from the original gastrula cavity of the young larva, and is lined by hypoblast.

Between the mouth and anus is a marked tongue-like projection, the **epistome**, which bears a tuft of very long cilia.

The **mesoblast**, **M**, consists of two lateral masses of rounded cells lying at the sides of the body between the œsophagus and the rectum; it is developed as in other Trochophore larvæ from two

**primary** or **polar mesoblast cells**, which are present at a very early stage between the epiblast and hypoblast at the hinder end of the body.

The **kidneys, K**, are a pair of short ciliated tubes, developed from the anterior end of the mesoblast masses.

The organ, **DO**, lying in front of the mouth, consists of a solid mass of cells (yellow), imbedded in which is a small flask-shaped depression of the external epiblast, lined by ciliated epithelium. The whole organ, spoken of by Balfour as the 'dorsal organ,' and regarded by Hatschek as a commencing bud, has been shown by Harmer to be a **nerve ganglion** with a sensory pit imbedded in it.

The later stages of development present some striking peculiarities. The larva, after leading for a time a free existence, attaches itself by means of the thickened ciliated præoral rim, so that both mouth and anus lose for a time their communication with the exterior. The whole alimentary canal now becomes rotated within the larva through almost  $180^{\circ}$ , and a mouth and anus are formed about the position marked **X** in the model, almost at the opposite pole of the body to that at which they were originally situated.

During this shifting, the internal organs undergo great changes: the terminal sense organ, **CD**, disappears, and parts of the nerve ganglion, **DO**, and of the alimentary canal are absorbed; while the neck of attachment gradually elongates to form the stalk of the adult.

The Trochophore larva is seen in its most characteristic form in Annelida (Models **3**, **4**, and **5**), in Mollusca (Model **6**), and in the Gephyrea chaetifera. In Polyzoa and in Rotifera it occurs in a less typical and more or less modified form.

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#### MODEL 8. Auricularia larva of Holothuria.

*The model is from the figures and descriptions of Professor Selenka,\* and is about 300 times the linear dimensions of the natural object.*

The eggs of Holothuria, like those of other Echinodermata, are small, and the early developmental stages are passed through rapidly.

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\* Selenka, "Zur Entwicklung der Holothuriën," *Zeitschr. Wiss. Zool.*, vol. 27, 1876.



By the end of the fourth day, the larva has reached the stage represented by the model.

In **general shape** the larva is somewhat fusiform; widest in the middle, and tapering towards both ends. The ventral surface is crossed about the middle of the length of the animal by a wide and and deep **transverse groove**, into which the mouth opens in the median plane.

The larva in its earlier stages is ciliated all over; at the stage represented by the model the **cilia** are restricted to a thickened rim, of a darker blue colour in the model, which borders the anterior and posterior lips of the transverse groove, and is prolonged on each side into loops extending to the anterior and posterior ends of the larva.

The **mouth**, a wide opening in the mid-ventral plane, at the bottom of the transverse groove, leads into a short **œsophagus**, **OE**, which opens into a **stomach**, **S**, divided by a constriction into proximal and distal portions, and continued as a short tubular **intestine**, **I**, to the **anus**, which is on the ventral surface, some way in front of the hinder end of the larva.

The sacs, **HC**, and **EC**, coloured yellow in the model, and lying along the left side of the alimentary canal, are the rudiments of the **ambulacral system** and of the **body cavity**. They are developed in the following manner.

At an earlier stage than that shown in the model, when the mouth is not yet formed, and the alimentary tract is a sac opening behind at the anus but ending blindly in front, a diverticulum arises from the blind anterior end of the alimentary sac and becomes constricted off as a closed vesicle. This vesicle moves to the left side of the alimentary tract, and shortly after the formation of the mouth, becomes divided into an anterior portion, **HC**, and a posterior portion, **EC**. These are connected for a time by a narrow stalk as shown in the model, but separate completely very shortly afterwards.

The **anterior vesicle**, **HC**, or **hydrocœl**, forms the commencement of the ambulacral system. It gives off a diverticulum, **MT**, the **madreporic tube**, which opens at the **dorsal pore**, **DP**, on the dorsal surface of the larva and about the middle of its length. In later stages the hydrocœl becomes horse-shoe shaped, its two limbs



embracing the œsophagus and ultimately meeting and fusing round it to form the **circumoral ambulacral vessel**. From this latter five outgrowths arise, the rudiments of which can be seen along the right side of the hydrocœl in the model, and which become the five **oral tentacles** of the adult. Five other outgrowths, arising at a slightly later stage, become the **radial ambulacral vessels** from which the **tube feet** arise as lateral diverticula. Ultimately the madreporic tube of the Holothurian separates from the dorsal surface and lies in the body cavity.

The **posterior vesicle, EC**, or **enterocœl**, divides into two, which encircle the hinder part of the stomach, **S**. In the later stages the cavities of the two enterocœlic vesicles dilate enormously and give rise to the two halves, right and left, of the body cavity of the adult.

The stellate cells (yellow) seen attached to the inner surface of the epiblast at various parts of the model are mesoblast cells: they are budded off at an early stage from the hypoblast of the alimentary canal, and are mainly converted into connective tissue and muscle. Some of these cells are seen in the model closely applied to the wall of the stomach, and already undergoing elongation to form the circular muscles of the adult stomach.

In the Holothurians the transition from the larva to the adult is a gradual one; but in most other Echinoderms there is a more or less marked metamorphosis. This is well illustrated for Asterids in the series of models showing the development of the starfish. The metamorphosis is still more abrupt and extensive in the Echinids and Ophiurids.

### MODEL 9. Tornaria larva of Balanoglossus.

*The model is from the figures and descriptions of Professor Johannes Müller,\* and is about 100 times the linear dimensions of the natural object.*

Balanoglossus is a worm-like animal, varying in length from half an inch to a foot or more according to the species, and found living in

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\* Johannes Müller, "Untersuchungen über die Metamorphose der Echinodermen: vierte Abhandlung," *Abhandl. Naturh. Wiss. Berlin*, 1851.

shallow water buried more or less completely in the sand of the sea bottom. It has attracted much attention because of its possession of a series of paired slit-like openings, leading from the alimentary canal to the exterior, which in their relations and mode of development closely resemble the gill clefts of *Amphioxus*.

In the earlier stages of development the most interesting feature is the occurrence of the larval form known as *Tornaria*, whose structure is shown in the model, which in some respects resembles the Trochophore larva of Annelids and Molluscs, and in others bears a striking resemblance to an Echinoderm larva.

The **Tornaria larva** is ovoid in shape: its ventral surface is crossed a little behind the middle of its length by a deep **transverse groove**, into which the mouth opens in the median plane. The lips of the groove form thickened transverse ridges, fringed with long **cilia**, and prolonged forwards to the anterior end of the body in a characteristic sinuous course. The posterior end of the larva is encircled by a transverse girdle of cilia, indicated by dots on the model.

The **mouth**, as already noticed, is in the floor of the transverse groove crossing the ventral surface: it is rather behind the middle of the body, so that fully half the larva is præoral in position. The mouth leads into a short curved **œsophagus**, **OE**, opening into a saccular **stomach**, **S**, from which an **intestine**, **I**, runs to the **anus** in the centre of the hinder end of the body.

At the anterior end of the larva, between the two ciliated ridges, is an epiblastic thickening, probably a **nerve ganglion**, with two **eye spots** imbedded in it, one of which is shown in the model. From this ganglion a band, described as contractile, but probably in part nervous in character, runs backwards towards the œsophagus.

The large thin-walled sac, **HC**, arises at an early stage as a diverticulum from the alimentary canal: it soon becomes constricted off, and at the stage shown in the model has acquired an opening to the exterior on the dorsal surface, **DP**. The upper, blind end of the sac is connected with the band arising from the apical ganglion. This sac in its mode of development resembles so closely the **anterior cœlom** of an Echinoderm larva that it is impossible to avoid the conclusion that they are corresponding structures.

The **body cavity** arises as two pairs of diverticula from the sides of the stomach, **EC** and **EC'**. These early separate from the stomach and form flattened sacs closely embracing its sides. The two sacs of each side open into each other, and then by further dilatation the anterior pair give rise to the body cavity of the collar region and the posterior pair to the body cavity of the trunk.

At the close of larval life there is a distinct metamorphosis by which the Tornaria larva is converted within a few hours into the adult Balanoglossus. In other species of Balanoglossus the Tornaria stage does not occur, and the young develop directly and without metamorphosis into the adult.

Description of a Series of  
Wax Models illustrating the Development of the

WATER BEETLE  
(*Hydrophilus piceus*).

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CASE CIV.

*The Models are by Dr. Ziegler, from the drawings and descriptions of Professor Kowalevsky\* and Dr. Karl Heider; and were made under Dr. Heider's personal direction.*

*The Models are in each case twenty-five times the linear dimensions of the natural objects.*

The great water beetle, *Hydrophilus piceus*, is one of the largest of our British beetles, measuring nearly two inches in length. The females lay their eggs in cocoons, which are attached to the under surface of floating leaves in the ponds which the beetles inhabit. Their cocoon is somewhat pear-shaped, measuring about  $\frac{3}{4}$  inch long by  $\frac{1}{2}$  inch wide, and is prolonged at one end into a pointed stalk, about an inch in length. It consists of an outer chitinous capsule, and an inner soft mass of silky threads in which the eggs are imbedded. The beetle takes about three hours to form the cocoon, spinning the silken threads from a pair of spinnerets at the sides of the anus.

The cocoon contains from forty-five to fifty eggs; these are about  $\frac{1}{4}$  inch long, and have the shape shown in the models. They are arranged in the cocoon side by side in rows like palisades, the larger

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\* Kowalevsky, "Embryologische Studien an Würmern und Arthropoden," *Mém. Acad. Sci. St. Petersburg*, vol. 16, 1871; Heider, "Die Embryonalentwicklung von *Hydrophilus piceus*," 1889.

or tail ends being directed upwards, and the narrower or head ends downwards. Each egg is enclosed in a fine silken web, serving to keep it in position. Above the eggs in the cocoon is a large air reservoir.

The cocoons are found in spring, very commonly about the second week of May. The eggs, which are fertilised as they are laid, by spermatozoa received by the female some weeks previously, commence to develop at once. In about twelve or fourteen days the young larvæ are fully formed, and working their way out of the egg membranes escape from the cocoon through an aperture at the base of the long pointed stalk.

The larva is very unlike the adult in appearance and in habits, being carnivorous and extremely voracious. It grows rapidly, and after reaching its full size, crawls out of the water, and, burying itself in the damp ground, becomes transformed into a pupa or chrysalis, from which the adult winged beetle, which is a vegetable feeder, in due time emerges.

The models illustrate the development of the larva during the first half of the time spent within the cocoon. Model 1 shows the stage reached shortly before the end of the second day from the time of laying of the eggs and formation of the cocoons : and Model 11 shows the condition at the end of the seventh day.

A brief account of the stages of development prior to that shown in Model 1, will facilitate the understanding of the series.

At the time the egg is laid it consists of a solid mass of yolk, invested by a thin outer layer of granular protoplasm, from which fine threads run inwards, branching and uniting with one another to form a protoplasmic reticulum extending through the substance of the yolk. In the surface layer of the protoplasm, nearer the larger or hinder end of the egg, and apparently in what will afterwards be the mid dorsal line of the embryo, is the small egg-nucleus or germinal vesicle. After fertilisation the nucleus divides rapidly into a number of small nuclei ; these at first lie in the yolk, but soon move outwards and become imbedded in the surface layer of the protoplasm, which becomes divided into cells, each containing one of the nuclei.

The egg now, about the end of the first day, consists of : (1) a solid central mass of yolk, traversed by a protoplasmic reticulum,

and having a few nuclei remaining imbedded in it; and (2) a superficial layer of nucleated epithelial, or epiblast cells, closely investing the entire yolk.

Development now pauses for a time, and very little further change occurs until towards the end of the second day, the next stage of importance being shown in Model 1. From this time development preceeds rapidly.

The ventral surface of the embryo and the organs situated on it are developed first: and even at the stage shown in Model 11, at the end of the seventh day, when all the appendages, and the mouth, anus, nervous system, and tracheal tubes are fully established on the ventral surface, the dorsal surface of the embryo has not yet commenced to form.

The colours of the models have the following significance:—

**Dark brown**:—The central mass of yolk; see Models 4 and 5.

**Yellow**:—The thin layer of epiblast cells investing the egg.

**White**:—The special thickenings of the epiblast, which give rise to the various organs of the embryo.

**Blue**:—The cut edge of the epiblast of the embryo in Model 5.

**Red**:—The cut edge of the mesoblast in Model 5.

In all the models the anterior or head end is turned upwards, the posterior end downwards, and the ventral surface towards the observer.

The ages given in the following descriptions date from the time of laying of the eggs.

#### MODEL 1. Egg 45½ hours after laying.

The white patches indicate the slight thickenings of the epiblast which mark the first commencement of the several parts of the embryo. The whole part coloured white may be spoken of as the **embryonal area**. The transverse white bands indicate the **segments**, of which the full number have not yet appeared; and the two crescentic white patches, **PL**, at the anterior end are the **procephalic lobes**, from which the anterior part of the head will be developed.

Behind the procephalic lobes is a slightly depressed median area, **G**, bordered by two prominent lateral folds; and at the hinder end of the embryo there is a similar, though less conspicuous area. These



depressed median areas, with their marginal folds, form the first commencement of the **germinal groove**, a structure which is seen more fully developed in Model 2.

It will be noticed that the embryo is at first almost confined to the posterior or wider half of the egg: in the succeeding stages, it rapidly extends forwards towards the anterior end.

**MODEL 2. Egg 47 hours after laying.**

Considerable advance has been made in development during the hour and a half that have elapsed since the stage shown in Model 1.

The **embryonal area** (white), is larger and more clearly defined.

The **germinal groove**, **GG**, is now a well pronounced median furrow, extending along the ventral surface of almost the entire length of the embryo. The lips of the groove have grown in towards each other: they have met and fused at the posterior end of the groove, and have nearly met along the greater part of its length. The lips present indentations corresponding to the **segments** of the body, the boundaries between which are indicated by transverse grooves. At the anterior end, and near the posterior end the germinal groove is more widely open than elsewhere.

Across the hinder end of the egg, immediately behind the place where the lips of the germinal groove have fused, is a deep crescentic depression. This is caused partly by the sinking of the hinder end of the embryo into the yolk, as is shown more fully in Models 3 to 5, and partly to the uprising of the posterior lip of the depression as a fold, the **amnion**, **AM**, which in the later stages rapidly extends forwards so as to cover over the embryo.

MODELS 3, 4, and 5 represent embryos of the same age, fifty-three hours from the time of laying of the eggs.

**MODEL 3. Egg 53 hours after laying.**

The lips of the **germinal groove** have met, and are fusing with each other along nearly the entire length of the embryo: at the anterior end a lozenge-shaped opening, **G**, still remains between them.

The **amnion**, **AM**, has advanced rapidly in development. Its first formed part, the **tail fold of the amnion**, has grown forward considerably, so as to cover over and conceal the hind end of the embryo. Its sides are continued forward as a pair of ridges, the **side folds of**

the **amnion**, bordering the embryo: these rapidly diminish in prominence, but become continuous in front with similar folds, the **head folds of the amnion**, which have commenced to grow backwards over the procephalic lobes, **PL**.

The amnion thus arises as a fold of the epiblast at the edge of the embryonal area, completely surrounding the embryo. Being formed as a fold, it will consist of two layers of cells, inner and outer; which may be spoken of respectively as the **inner amnion fold**, lying next to the embryo; and the **outer amnion fold**, lying just beneath the vitelline membrane that encloses the whole egg. The amnion is merely an embryonic membrane: it forms no part whatever of the embryo itself, and disappears completely at a later stage. In its mode of formation, its relation to the embryo, and its ultimate fate the amnion of an insect bears a strong resemblance to the amnion of a vertebrate, such as a chick or rabbit. The two structures are, however, perfectly distinct, and do not correspond to each other morphologically.

In the embryo the several **segments** may already be identified. The **mandibular segment**, **MN**, is imperfectly bounded in front: behind it come the **first and second maxillary segments**, **MX 1**, **MX 2**; the **three thoracic segments**, **T 1**, **T 2**, **T 3**; and the **first two abdominal segments**, **A 1**, **A 2**. The hinder abdominal segments are concealed by the amnion.

**MODEL 4.** The ventral half of an egg of the same age, **53 hours**, as **Model 3**.

The egg has been divided by a longitudinal section, and the dorsal half removed. From the remaining, or ventral half, the yolk has been removed on the right side to show the relations of the embryo.

The most important point shown by the model, as compared with **Model 3**, is the way in which the **tail end** of the embryo, **TN**, grows round the broad end of the egg, burrowing in the yolk, and completely hidden from the surface. The structure and relations of the tail end are better seen in **Model 5**.

**MODEL 5.** Portion of an egg of the same age, **53 hours**, as **Models 3 and 4**.

The egg has been cut across through the middle of the first maxillary segment, and the anterior half removed. From the remaining portion the dorsal half has been removed, except at the extreme hinder end, by a couple of cuts, longitudinal and transverse respectively. The embryo is cut across twice, once (**A**) on the ventral surface of the egg, and once (**B**) on the dorsal surface near the hind end of the egg; compare Model 4. In these sections the epiblast of the embryonal area, forming the ventral surface of the embryo, is coloured blue; and the mesoblast is coloured red.

SECTION A, at the upper end of the model, passes through the middle of the first maxillary segment. In the median plane is seen the **germinal groove**, the lips of which have just met to complete the tube. This **tube**, the walls of which are coloured red in the model, separates completely, at a slightly later stage, from the epiblast (blue), and spreads out laterally between the epiblast and the yolk. Its walls become the **mesoblast** or middle germinal layer of the embryo, and according to Heider give rise also in part to the **hypoblast** or inner germinal layer. The cavity of the tube becomes obliterated along the median plane, but persists laterally in each of the segments of the body as a pair of cavities which form the **primitive cœlom** or body cavity. These do not, however, become the **definite body cavity** of the adult insect, which is formed by enlargement of a series of lacunar spaces which arise independently and apparently belong really to the vascular system.

The embryonal area (blue), is bounded laterally by the side folds of the **amnion**, which in this region are as yet, compare Model 3, a pair of very low ridges formed by folding of the epiblast.

SECTION B, on the dorsal surface of the hinder end of the model passes through the tail end of the embryo, which, as shown in Model 4, has grown round the hinder end of the egg to its dorsal surface, burrowing in the yolk, and covered over by the tail fold of the amnion.

The **epiblast** of the embryonal area, forming the ventral surface of the embryo, is coloured blue. In the median plane, and dipping into the yolk, is the **germinal groove** (red), the lips of which have not yet met. The white layer facing the embryo, and continuous with the edge of the embryonal area (blue), is the **inner amnion fold**:

the **outer amnion fold** is directly continuous with the surface epiblast of the egg. Between the outer and inner amnion folds a thin layer of **yolk** (brown) is seen to have extended: the tail end of the embryo is consequently separated from the surface by the two layers, inner and outer, of the amnion, together with the stratum of yolk that has passed in between these two layers.

**MODEL 6. Egg 55 hours after laying.**

During the two hours between the stages shown in Models **3** and **6** the **amnion** has spread rapidly, so that the embryo is almost enclosed by it, an oval patch at the head end alone remaining exposed. Comparison with Model **3** shows that while the head and side folds of the amnion take some share in this growth, it is the tail fold, **AM**, that is by far the most active in the process.

The **embryonal area** (white) has slightly increased in length: and has shifted forwards so that the head is nearer the anterior end of the egg than before, and the tail no longer extends on to the dorsal surface of the egg: compare Model **4**.

Owing to withdrawal of the yolk from between the two layers of the amnion, compare Model **5**, the **amnion** is thinner and more transparent than before, and the several segments of the abdominal region, which now lie nearer the surface, are clearly visible through it.

**MODEL 7. 62 hours after laying.**

The **amnion** is almost complete, a small round hole at the anterior end, opposite the antennae, **AN**, alone remaining open. Except at this spot, the whole ventral surface of the embryo is covered by the two layers of the amnion, which are now very thin and transparent. In the model the several parts of the embryo are supposed to be seen through the amnion.

The **embryonal area** has extended forwards along the whole length of the ventral surface of the egg, the head reaching to the anterior end, while the tail, **TN**, has shifted round from the dorsal surface, compare Model **4**, and now lies on the ventral surface of the posterior end of the egg.

The division of the embryonal area into **segments** by transverse grooves is very evident. The full number of segments is now present: the embryo consisting of an anterior or **procephalic portion**, **PL**,

a series of **sixteen pairs of segments**, and a terminal portion or **telson, TN**. The procephalic portion and the telson differ in many respects from the segments, and appear to be, as in Annelids, of different morphological value to these.

The **procephalic portion, PL**, forms a broad, somewhat heart-shaped plate at the anterior end of the embryo: near its hinder border in the middle line is the small round hole where the amnion has not yet closed.

The **first three postcephalic segments, MN, MX 1, MX 2**, are small: they give rise to the hinder part of the head of the adult and from them the three pairs of jaws, **mandibles, first maxillæ**, and **second maxillæ**, are developed.

The next three or **thoracic segments T 1, T 2, T 3**, are the widest of the series. They become respectively the **prothorax, mesothorax**, and **metathorax** of the adult.

The **abdominal segments, A 1 to A 10**, decrease in size from before backwards; the first, **A 1**, being as large as a thoracic segment, while the last, **A 10**, is the smallest of the whole series.

The **telson, TN**, is an oval unsegmented plate, forming the posterior end of the embryo.

The rudiments of the **antennæ, AN**, are present as a pair of small rounded, backwardly directed processes from the sides of the procephalic region. There are as yet no traces of any of the other appendages.

Running along the whole length of the ventral surface of the embryo, except the procephalic region and the telson, is a median longitudinal groove: this is bordered by a pair of longitudinal ridges, caused by thickenings of the epiblast, which form the two halves of the **ventral nerve chain**. The ridges are from the first slightly dilated opposite the middle of each segment at the places where the **ganglia** will be formed later: and slightly constricted opposite the intersegmental grooves.

#### MODEL 8. Egg 82 hours after laying.

The **amnion**, which is left in position, forms a thin transparent double membrane, investing the whole of the embryonal area. Through it the appendages and other parts of the embryo can be seen.



**MODEL 9.** Egg of the same age, 82 hours, as **Model 8**.

The amnion has been removed so as to expose the embryo fully.

The **embryonal area** has increased in width, especially at its anterior end. The **procephalic area**, **PL**, has extended round the anterior end of the egg on to its dorsal surface; the transverse crescentic depression, **S**, with thickened lips, near its hinder border is the commencing **stomodæum**, or anterior portion of the alimentary canal.

The **antennæ**, **AN**, have increased in size as compared with **Model 8**, and now form prominent rounded buds, projecting slightly backwards from the sides of the hinder border of the procephalic region. It should be noticed as an important point, that the antennæ lie at this stage behind the level of the stomodæum or mouth opening.

The several **segments** are even more clearly marked off from one another than in **Model 7**. The full number is present; and the hinder abdominal segments, **A 9** and **A 10**, though still the smallest of the series are considerably larger than at the earlier stage.

**Appendages** are now present on nearly all the segments. They appear as paired, rounded processes from the hinder borders of the segments, and almost from the first have different shapes in the several regions of the body. They consist at first merely of hollow buds of epiblast, but as they increase in size the mesoblast soon extends into them.

Of the three pairs of **mouth appendages** the **mandibles**, **MN**, are of moderate size; the **first maxillæ**, **MX 1**, are distinctly larger; and the **second maxillæ**, **MX 2**, are the smallest of the three. It should be noticed that the mouth appendages and the antennæ lie in line with one another, and appear to belong to the same series of structures.

The appendages of the **three thoracic segments**, **T 1**, **T 2**, **T 3**, are well developed, and of approximately equal size, the prothoracic appendages being slightly smaller than the others. The thoracic appendages are more flattened and more backwardly directed than the mouth appendages.



The **first abdominal segment, A1**, bears a pair of appendages of the same shape as those of the thoracic segments, but of much smaller size: and rudiments of appendages in the form of small rounded processes are present on all the succeeding abdominal segments, except the last or tenth, **A 10**.

The **telson, TN**, bears no appendages, but presents about the middle of its length a transverse crescentic depression, which is the commencement of the **proctodæum**, or posterior portion of the alimentary canal.

At the bases of the appendages of the second thoracic segment, **T 2**, are a pair of oblique grooves, **SP**; these are the **spiracles** or **stigmata**, the commencements of the tracheal system, and are better seen in the next model.

The median longitudinal groove along the ventral surface is well seen, commencing immediately behind the stomodæum, **S**, and extending to the last abdominal segment. Bordering the groove are the two **nerve cords**, which are thickened opposite the middles of the segments to form the **ganglia**, and are especially prominent in the head and thoracic regions.

#### MODEL 10. Egg 94 hours after laying.

The **embryonal area** has widened considerably, especially in the abdominal region: it has, however, diminished in length, and is now confined to the ventral surface of the egg, not reaching either of its ends.

The **amnion** has been removed.

The **procephalic region, PL**, is greatly reduced in size: it forms a rounded prominence, at the base of which is the mouth, **S**: this has shifted slightly backward and now lies distinctly behind the basis of the antennæ, **AN**.

The **embryonal area** is of approximately uniform width along the greater part of its length, tapering at the two ends: the increase of width in the abdominal region, as compared with Model 9 is very noticeable. There is as yet no clear division of the body into head, thorax and abdomen; and the largest segments are the anterior four or five abdominal ones.

The **telson, TN**, is smaller than in Model **9**, and, owing to the shortening of the embryonal area, lies rather between than behind the two halves of the tenth abdominal segment. The **proctodæal** or **anal opening** is a tranverse depression in the telson, immediately below the letters **TN**.

The **antennæ, AN**, have increased considerably in length, and are now directed backwards and inwards along the sides of the procephalic region. As already noticed, the bases of the antennæ are now situated in front of the level of the mouth.

The **mandibles, MN**, are short, stout appendages; each is notched at its posterior border into three teeth.

The **first maxillæ, MX 1**, are of considerable size: each is notched at its posterior border, and gives off a backwardly directed process, overlapping the second maxilla.

The **second maxillæ, MX 2**, are much smaller than the first maxillæ, and partially overlapped by them; in shape they are not much unlike the thoracic legs.

The **appendages of the three thoracic segments, T 1, T 2, T 3**, are stout conical processes directed backwards and slightly inwards, and imperfectly divided into joints by transverse constrictions. The first thoracic appendage is the smallest of the three, and the third is the longest.

The **first abdominal segment, A 1**, has a pair of distinct appendages in the form of small, backwardly directed processes, seen in the model immediately behind the tips of the third thoracic appendages. The **hinder abdominal segments**, from the second to the ninth, **A 1 to A 9**, inclusive, have rudimentary appendages in the form of rounded processes of their hinder borders, similar to and in line with the appendages of the first abdominal segment, but of much smaller size.

The **tenth abdominal segment, A 10**; and the **telson, TN**, bear no appendages.

**Spiracles or stigmata, SP**, are present as a pair of transverse or slightly oblique slits on the ventral surface of each of the segments from the second thoracic, **T 2**, to the eighth abdominal, **A 8**, inclusive. Each spiracle leads into a flattened **tracheal sac**.

The median ventral groove, and the **ganglionated nerve cords** bordering it, are very conspicuous in the model. The ganglia of the several segments are still quite distinct from one another; and in front of the anterior or mandibular ganglia the **para-oesophageal commissures** may be seen running forwards at the sides of the mouth, and close to the inner borders of the antennæ.

**MODEL 11. Embryo at the end of the seventh day.**

The **amnion** has been removed.

The most noticeable changes, as compared with Model 10, are (1) the great enlargement of the head region, which has spread over the anterior end of the egg on to its dorsal surface; (2) the presence of a marked constriction between the head and the first thoracic segment; (3) the great increase in size of the thoracic segments and their appendages.

The **mouth, S**, is now a wide transverse slit at the extreme anterior end of the embryo, bordered by well-marked upper and lower lips. Behind the upper lip, on the dorsal surface of the head is the commencing **clypeus, C**.

The **head** has greatly increased in size, and is now acquiring its characteristic shape; the segments forming it have completely fused with one another. On the ventral surface and sides the head is separated by a deep groove from the first thoracic segment.

The three **thoracic segments** are of great size, and are separated from one another by deep constrictions.

The **first abdominal segment, A 1**, is very similar to a thoracic segment; the **hinder abdominal segments** are very wide, but gradually diminish in length towards the posterior end of the body. The **last abdominal segment, A 10**, consists of two separate halves, lying at the sides of the telson, and almost completely surrounding it.

The **telson, TN**, is small, and perforated by the slit-like **procto-dæal opening**.

The **antennæ, AN**, have shifted forwards, and now form a pair of short, curved, downwardly directed processes, situated entirely in front of the mouth.

The **mandibles, MN**, have also shifted forwards, and now lie at the sides of the mouth. They have rotated so that their notched or toothed margins, which were previously, Model **10**, directed backwards are now turned inwards towards the median plane.

The **first maxillæ, MX 1**, are of great size, and lie some little distance behind the mandibles.

The **second maxillæ, MX 2**, are similar in shape to the first maxillæ, but are of much smaller size, and are partly overlapped by these.

The **three pairs of thoracic appendages, T 1, T 2, T 3**, which become the three pairs of legs of the adult insect, have increased considerably in size and are clearly divided into joints by transverse constrictions.

The **first abdominal segment, A 1**, still bears a pair of conspicuous, knob-like appendages : but the appendages of the **hinder abdominal segments, A 2 to A 9**, though still present, are of very insignificant size.

**Spiracles, SP**, are present as before in pairs on the sides of the segments from the second thoracic, **T 2**, to the eighth abdominal, **A 8**, inclusive : they are now circular in outline, with slightly raised lips.

The **tracheal sacs** into which the spiracles lead have now opened into one another, so as to form a pair of longitudinal air sacs from which the **tracheal tubes** arise, supplying the several parts of the body.

The two halves of the **ventral nerve chain** are clearly visible in the abdominal region, though rather less conspicuous from the surface than in Model **10**. In the thoracic and cephalic regions they are more deeply placed, and are, in addition, concealed by the appendages.

On the dorsal surface of the head, the swellings caused by the **supra-œsophageal ganglia**, or "brain," **B**, are well seen.

About the stage represented by Model **11**, the annion splits longitudinally along its entire length in the median plane, and the two halves rapidly shrink away from each other towards the dorsal surface,

thus exposing the ventral surface of the embryo. The embryonal area, by further increase in width, gradually spreads round the sides, and ultimately covers the dorsal surface of the egg; thus completing the wall of the embryo. The shrivelled remains of the amnion are carried up to the dorsal surface of the embryo by the spreading of the embryonal area, and ultimately disappear.

The mass of the yolk, which occupies the interior of the egg, compare Models 4 and 5, is gradually enclosed by the formation of a definite layer of cells, the hypoblast, around it. The hypoblast cells form the lining epithelium of the middle portion of the alimentary canal, the anterior and posterior ends being formed by the stomodæum and protodæum respectively. The mass of the yolk thus ultimately lies in the interior of the alimentary canal, where it is gradually absorbed and digested.













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